Multi-taxa functional diversity in UK plantation forests

Kirsty Godsman MSc

Edge Hill University

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Contents

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Abstract

Anthropogenic pressures are leading to biodiversity loss on a global scale at a rate that is comparable to that of historic mass extinctions and this threatens the functioning of stable and healthy ecosystems. Forests play a major role in supporting biodiversity, however, deforestation continues to occur at an alarming rate. It is increasingly recognised that plantations can have a role in supporting biodiversity and delivering many of the ecosystem functions of natural woodland and sustainable forest management guidelines have been developed to ensure this. However, the evidence base for these guidelines is limited and further research is required.

A multi-taxa approach is needed to make effective, informed decisions on the management of habitats for biodiversity conservation. Further, functional ecology has the potential to improve our understanding of the mechanisms underlying ecosystem change since it more directly relates to response to environmental gradient and ecosystem functioning. This study explores multi-taxa (vascular plant, moss, carabid and spider) functional and taxonomic diversity across 40 study plots of typical forests in order to assess the ability of these forests to support biodiversity throughout the forest harvest cycle and over the long-term.

Common forest types, including non-native plantation, native plantation and native forest, were found to have a role in supporting biodiversity, including species of conservation concern. However, this varied in Sitka spruce forests, with closed-canopy stages of the forest harvest cycle supporting less diverse communities. In addition, long-term declines in

diversity were detected in all forest types, but this varied with taxonomic group. Overall, canopy tree species was not as important as stand structure or location in determining community composition and diversity, suggesting that alternative management could be implemented to improve a forest's ability to support biodiversity.

Key words: Forest; Plantation; Sustainable forest management; Vascular plant; Moss; Carabid; Spider; Multi-taxa; Functional ecology

Chapter 1

Introduction

Biodiversity loss

Biological diversity, or biodiversity, is the variety of species, functional traits or genes within and between ecosystems. There is a significant growing body of evidence suggesting that anthropogenic pressures are leading to the loss of biodiversity on a global scale at a rate that is comparable to that of historic mass extinctions (Barnosky et al., 2011; Ceballos et al., 2015). Further, biotic homogenisation (the increasing taxonomic, functional or genetic similarity of different communities over time) has been identified as an important part of the current global biodiversity declines (Olden et al., 2018). Biotic homogenisation results from both the spread of invasive species and the loss of rare species due to, for example, intensification of land-use, habitat change and climate change and could have important consequences for the resilience of ecosystem functioning (Olden et al., 2004). Perhaps one of the most compelling arguments for halting this biodiversity loss is that all living things contribute to the functioning of stable and healthy ecosystems which provide valued ecosystem services to humanity (Hooper et al., 2005). Ecosystem services include, for example, nutrient capture and cycling, pest control, recreation, food production and climate regulation (MEA, 2005; Soliveres et al., 2016). There is now evidence that biodiversity can have a positive effect on these ecosystem services and more biodiverse ecosystems can have greater resilience to environmental change due to complementarity of species responses and an “insurance effect” (Balvanera et al., 2006; Hooper et al., 2005). Biodiversity loss itself has been indicated as a major driver of ecosystem change, with the rate accelerating as biodiversity loss continues (Cardinale et al., 2012). Recognition that the simplification of ecosystems to enhance resource provision has led to biodiversity loss and is not sustainable in the long-term (Cardinale et al., 2012) led to the creation of the Convention on Biological Diversity (CBD) (United Nations, 1992). As part of this, 196

countries were signatories to the CBD and are legally obliged to ensure the conservation and sustainable use of biological diversity across all ecosystems.

Forest biodiversity

Forests play a major role in supporting biodiversity through the direct provision of habitat but also in the provision of ecosystem services such as timber and wood production, water and soil protection, carbon sequestration and recreation (Balvanera et al., 2014; FAO, 2015). However, deforestation continues to occur at an alarming rate (FAO, 2015) (Table 1.1). Prompted by the CBD, sustainable forest management principles (SFM) were developed. The purpose of SFM is to guarantee that forests are used in a way that ensures the maintenance of biodiversity, productivity, regeneration capacity, vitality and social functions and do not damage other ecosystems in the process. As a result of this, SFM approaches were established to provide forest practitioners with practical guidelines with which to achieve SFM (e.g. FSC Stewardship). However, it has been suggested that the evidence base for this guidance is limited (Puri et al., 2016).

Table 1.1: Global forest cover, including a breakdown of forest cover by forest type and the annual change in cover of each. Natural forest comprises forest that has never been influenced by humans. Plantation forest includes forests of planted origin only. Production forest may or may not be of planted origin but includes all forest that have timber products extracted.

	Global forest cover	Natural forest	Managed purely for conservation	Plantation forest	Production forest
Area	3999 million ha (30.6% land area)	3695 million ha (93% forest area)	524 million ha (13% forest area)	291 million ha (7% forest area)	1187 million ha (30% forest area)
Trend since 1990	↓ 0.13% per annum	↓ 0.24% per annum	↑ 1.75% per annum	↑ 1.84% per annum	~

The global rate of deforestation has decreased over the last 25 years, but this is, in part, due to an increase in the area of plantation forests (FAO, 2015). The term plantation forest refers to forests of planted origin rather than of natural regeneration from seed and these provide an alternative to extracting timber from natural forests (Schuck et al., 2002). Plantation forests are commonly managed by clearfell harvesting and replanting of trees, often of non-native origin. Clearfelling refers to the removal of the overstorey of an entire

stand at once (Schuck et al., 2002). This is one of the most common silvicultural practices for plantation forests globally, though alternatives such as retention, and selection systems are also used to a lesser degree (Chaudhary et al., 2016).

Clearfell represents a major disturbance in forest ecosystems. Although forests are subject to natural disturbance regimes which occur across many different spatial scales including fire, windthrow, pest outbreaks and natural tree death, disturbance from clearfelling is different to that of natural forests (Lindenmayer and McCarthy, 2002). After harvesting, trees are re-planted at higher densities than occur through natural regeneration, with large areas planted at the same time. This results in single-aged, uniformly structured stands, especially where only one tree species is planted (Carnus et al., 2006). In addition, harvesting usually occurs long before the trees reach ecological maturity (Brockerhoff et al., 2008). Consequently, important characteristics of forest structure, tree species and successional dynamics may be altered in areas where plantations have replaced natural forests. For this reason, plantation forests have historically not been considered equivalent to natural forests in terms of their ability to support biodiversity and, therefore, ecosystem functions and services (Stephens and Wagner, 2007). However, with research, our understanding has developed and it is increasingly recognised that plantations can have a role in supporting biodiversity and delivering many of the ecosystem functions of natural woodland (Bremer and Farley, 2010; Chaudhary et al., 2016; FAO, 2015; Irwin et al., 2014; Paillet et al., 2010; Quine and Humphrey, 2010). Further, the role of plantation forests in supporting biodiversity and forest-related ecosystem functions and services may be especially important in regions where they represent the main forest cover and where ecosystems in general are degraded (Bremer and Farley, 2010; O'Callaghan et al., 2017; Quine and Humphrey, 2010).

Plantation forests in the United Kingdom

The United Kingdom (UK) is thought to have been a predominantly forested island around 9000 years ago, following the retreat of ice sheets about 11000 years ago. This forest has been gradually deforested by humans over the past 4000 years (Atkinson and Townsend,

2011). Around 1000 years ago, forest cover had declined to around 15% and by 1905 had declined further to just under 5% (Forest Research, 2019). Shortly after this, the Forestry Commission was formed and began a large-scale programme of tree planting to recover timber stocks. Since this was motivated by timber production, the trees planted were mainly fast-growing, non-native conifers planted in monocultures (Atkinson and Townsend, 2011). The most recent estimates suggest that forest cover in the UK now represents 13% of the total land area and continues to increase (Forest Research, 2019). However, this is low in comparison to estimates for Europe where forest cover represents 33% of the land area (FOREST EUROPE, 2015). In addition, UK forests comprise a large proportion of plantation forest (roughly 80% in the UK compared to 9% in European forests) relative to that of semi-natural or natural forest (Atkinson and Townsend, 2011; FOREST EUROPE, 2015). Although there does not appear to be a single definition for natural or semi-natural forests, they are generally considered to consist of native tree species, originating from natural regeneration and showing no indication of human activity or disruption of natural processes. Natural forests specifically should have never been used by humans. However, others have less strict definitions for these forest types and would include, for example, forests of planted origin which have undergone natural succession as well as those that still have anthropogenic influences (Peterken, 2019; Schuck et al., 2002). As previously mentioned, the proportion of forest cover is increasing in the UK and this is mainly due to increases in the rate of planting as a result of grant funding rather than natural regeneration and expansion of forest areas (Forest Research, 2019). Therefore, plantations contribute significantly to forest habitats in the UK and are likely to continue to do so. Hence, it is important to understand how this forest type contributes to the conservation of biodiversity and whether SFM approaches enhance their ability to do so.

The Forestry Commission first introduced the UK Forestry Standard in 1998 with the purpose of advising forest managers on the delivery of SFM within the unique context of UK forests, based on criteria set at the international level (Forestry Commission, 2017). Advice

includes: manage forests in a way that conserves or enhances biodiversity, improve the ecological connectivity of the landscape for forest species, maintain a maximum of 75% of a forest management unit as a single species, consider alternatives to clearfell systems, identify sites for long-term forest retention and control invasive species (Forestry Commission, 2017). The UK Forestry Standard also prioritises native forests and structural diversity for their perceived importance to biodiversity (Forestry Commission, 2017). Again, there is a limited evidence base and the advice can lack a prescriptive approach although the document is updated to take into account advances in scientific understanding (Forestry Commission, 2017; Puri et al., 2016). Therefore, there is still a need for a better understanding of how plantation forests support biodiversity and how this is affected by forest planning and management. Furthermore, how forest management and planning interact with climate change and wider habitat change to affect biodiversity is still poorly understood.

Studying biodiversity

Given the broad scope of the term biodiversity, it can be complex to measure (Magurran, 1988). For simplicity, we will refer only to the diversity of species, but the same principles can be applied to the diversity of genes, functional traits or ecosystems. In its most simple sense, biodiversity is measured as the number of unique species in a community (species richness). By taking account of both the number of species and the abundance of each, we can also get a better understanding of the evenness of diversity (a range of species diversity indices often collectively referred to as species diversity) (Magurran, 1988). The above measurements represent alpha diversity. Beta diversity, on the other hand, measures the change in alpha diversity between different communities and is useful for detecting patterns of change across space and time. We can also measure gamma diversity, or the total diversity across a pre-determined region (Whittaker, 1972). This relates to alpha and beta diversity because, where beta diversity is low (or different communities within a region are similar) alpha diversity will be similar to gamma diversity. However, if we only value sites

with the highest number of species, we would misinterpret the value of many habitats and communities. For instance, some habitats have low species richness but support unique species assemblages or species of conservation concern (Vitt et al., 1995). In addition, individual species can have a disproportionately large effect on ecosystem function (Paine, 1995). Therefore, the identity of species should be valued.

In recent years, biodiversity research has moved beyond simply quantifying taxon diversity to exploring other aspects of how a community responds to change, such as guild structure, niche breadth or functional traits (e.g. Uetz, Halaj and Cady, 1999, Thuiller, Lavorel and Araújo, 2005, Martello et al., 2018). A functional trait is any morphological, physiological, biochemical, behavioural or phenological characteristic of an individual that is related to its performance or fitness (Cadotte et al., 2011; Violle et al., 2007). Anything that cannot be measured at the individual level and/or is related to, for example demographics or environmental association or range size is not considered a functional trait (Violle et al., 2007). Trait types have been split into two main types: effect traits and response traits. The former includes traits related to the effects of an individual on environmental conditions, communities or ecosystem processes (Violle et al., 2007). Response traits, on the other hand, relate to an individual's response to changes in environmental conditions (Violle et al., 2007). The main advantages of the functional trait approach over the species-based approach are that functional traits are directly related to response to environmental gradient, species interactions and contribution to ecosystem functioning (Meiners et al., 2015). Also, since it does not use species identities which can vary between regions, the functional trait approach provides a common currency for large-scale studies, meta-analyses and comparative ecology, thus having the potential to improve understanding of the underlying principles of community assembly (Cadotte et al., 2011).

Diversity of functional traits can be measured in multiple ways. Numerous functional diversity indices have been developed for this purpose including functional richness, functional evenness, functional divergence and Rao's quadratic entropy, which is

analogous to Simpsons D (Botta-Dukát, 2005; Mason et al., 2005). Similarly to the different indices of species diversity, these account for the range of trait values, their frequency or combinations of the two. As a functional equivalent to community composition, it is possible to identify the dominant trait values within communities as well as the relative frequency of all possible trait values within communities (Shipley et al., 2011). This is referred to as the community weighted mean (CWM).

The selection of functional traits in analyses has important consequences in functional ecology. Villéger et al., (2008) demonstrated that species richness can influence some functional diversity metrics. In particular, inaccurate measurements of functional richness are obtained when species richness is low relative to the number of traits selected. Therefore, it is suggested that trait selection is limited so that species richness increases exponentially in relation to the number of traits selected, especially when making comparisons between communities (Villéger et al., 2008). Since the number of traits selected is limited by the species richness of a community, and for principles of parsimony, care should be taken to avoid trivially correlated traits (Maire et al., 2015; Petchey and Gaston, 2006). Perhaps most important is the *a priori* selection of only traits that are known to relate to the function(s) or environmental gradient(s) of interest (Petchey and Gaston, 2006; Violle et al., 2007).

Multi-taxa approach

Due to rapid declines in global biodiversity, there has been interest in the use of surrogate or indicator groups (e.g. well studied taxa such as birds and vascular plants or target species such as forest specialist species or species of conservation concern) to quickly and cost-effectively improve our understanding of the impacts of habitat change on other taxa, particularly those which are expensive to sample or for which ecological or taxonomic knowledge is limited (Burrascano et al., 2018; Larrieu et al., 2018). However, this has not been as effective as was hoped and it is suggested that a multi-taxa approach, where multiple taxonomic groups are studied in the same system, is required in order to make

effective, informed decisions on the management of habitats for biodiversity conservation (Aubin et al., 2013; Burrascano et al., 2018; Irwin et al., 2014; Sabatini et al., 2016). Focussing on single taxonomic groups has led us to underestimate the importance of biodiversity to ecosystem services (Soliveres et al., 2016). In addition, this approach assumes a similar response to the same environmental gradient between multiple taxonomic groups. However, this has rarely been found to be the case and any correlations between taxa have been weak (Aubin et al., 2013; Irwin et al., 2014; Larrieu et al., 2018). Larrieu et al. (2018) recommend the inclusion of at least two to three taxa can greatly improve the effectiveness of taxon surrogacy and Soliveres et al. (2016) add that multiple trophic levels should also be included. This will allow results to better represent the ecosystem, whilst also minimising the resources required to sample many more taxonomic groups.

The multi-taxa approach has become increasingly valued and, therefore, there are a growing number of studies exploring the response of multiple taxa to forest type and forest management (Aubin et al., 2013; Hilmers et al., 2018; Irwin et al., 2014; Penone et al., 2019; Quine and Humphrey, 2010; Schall et al., 2018). However, the same taxonomic biases exist in forests as elsewhere (e.g. vascular plants and vertebrates) (McKinney, 1999; Titley et al., 2017) and it is common for studies to focus on a small range of stages of forest succession (Hilmers et al., 2018). Moreover, due to the large number of forest types and management systems globally as well as the complexity of this habitat, there is still a lack of consensus on how forest management and commercial plantation forests affect biodiversity and ecosystem function (Hester et al., 2019).

Research Aims

This thesis aims to address this knowledge gap by exploring multi-taxa functional and taxonomic diversity across a range of typical forest types. Specifically, the thesis aims to:

1) determine the effects of environmental filtering on the functional diversity of four taxonomic groups (ground vascular plants, ground bryophytes, carabids and ground-active spiders) across full forest harvest cycles in two common plantation types in Great Britain (Chapter 2).
2) investigate long term changes in functional and taxonomic diversity of three taxonomic groups (ground vascular plants, ground bryophytes and carabids) in three common forest types in Great Britain to understand if biotic homogenisation has occurred in these communities over the past 20 years (Chapter 3)
3) undertake the first large-scale study of spider diversity in common forest types across Great Britain in order to better understand what drives community composition in these habitat types (Chapter 4)
4) contribute to the evidence-based SFM of plantation forests (Chapter 2-5).

Chapter 2

The role of environmental filtering in driving multi-taxa species and functional diversity through the plantation forest harvest cycle

Introduction

Global biodiversity declines reflect the increasing pressures many ecosystems are facing in the Anthropocene (Hallmann et al., 2017; Pimm et al., 1995; Sala et al., 2000; Sánchez-Bayo and Wyckhuys, 2019; Vitousek et al., 1997). As one of the most biologically diverse ecosystems in the world, forests play an important role in the provision of ecosystem functions such as nutrient cycling and carbon sequestration and it is now understood that biodiversity plays an important role in the provision of these ecosystem functions (Balvanera et al., 2014; Cardinale et al., 2012; Hooper et al., 2012; Meyer et al., 2016). Sustainable management of forest biodiversity is, therefore, important for healthy, functioning ecosystems that are resilient to global environmental change. Forests also deliver economically valuable ecosystem services such as wood production, climate change mitigation and recreation (European Environment Agency, 2016; FAO, 2015).

Global forest cover has been estimated at 30.6% of the total land area and, although the rate of deforestation has decreased, forest loss is still substantial (~ 0.13% per year) (FAO, 2015). The slowing rate of deforestation is, in part, due to the expansion of commercial plantation forests (FAO, 2015; FOREST EUROPE, 2015). These plantations are not considered equivalent to natural forests in terms of their ability to support biodiversity. This is because they may be composed of non-native tree species and are subject to different and more uniform disturbance regimes. They also typically have more uniform structure, particularly if planted in monocultures (Paillet et al., 2010). However, it is increasingly recognised that plantations can have a role in supporting biodiversity and in the delivery of many of the biodiversity-associated functions of natural forest, particularly in regions with low natural forest cover or where ecosystems in the landscape are degraded (Bremer and Farley, 2010; O'Callaghan et al., 2017; Paillet et al., 2010; Pawson et al., 2008; Quine and Humphrey, 2010).

In plantation forestry, clearfelling and replanting of single-aged monocultures is a widely practiced silvicultural strategy. Under this management system, clear-fell represents a major disturbance involving the near complete removal of the canopy and significant ground disturbance. This leads to a sudden influx of light, increased ground temperatures, reduced humidity, reduced soil moisture and loss of tree-related resources such as litterfall (Humphrey et al., 2003). Clear-felled stands are then re-planted, and the stand gradually begins to return to a closed canopy forest. This is accompanied by reduced light and increased humidity and soil moisture. These changes directly affect primary producers and both directly and indirectly affect higher trophic levels (Penone et al., 2019). This is a key environmental filter in forest ecosystems, though it occurs over a much shorter time period in plantations than in natural forest cycles, particularly for fast-growing, densely planted species.

Changes in faunal and floral species assemblages through the commercial forest harvest cycle have been relatively well documented and have been linked with these significant environmental changes. For instance, open-habitat species will typically decline through the forest harvest cycle with a corresponding increase in species associated with closed-canopy forest conditions (Bartha et al., 2008; Irwin et al., 2014; Mullen et al., 2008; Oxbrough et al., 2005; Purchart et al., 2013). Overall, diversity usually has a 'U-shaped' distribution through the forest harvest cycle, declining over time because increasing canopy cover is such a strong environmental filter, it reduces resources for all but the most shade-tolerant species. Later in the forest harvest cycle, the canopy reopens due to thinning operations or natural gaps beginning to form, resulting in increasing diversity (Jukes, Peace and Ferris, 2001, Smith et al., 2008, Purchart et al., 2013, Hilmers et al., 2018).

There has been comparatively limited research on the functional diversity (FD) of taxa through a forest harvest cycle. This is despite evidence that functional composition may be disconnected from taxonomic composition and may not follow a similar pace of recovery following disturbance (Aubin et al., 2013; Fountain-Jones et al., 2017). FD is defined as the

identity, range and distribution of functional traits of organisms in communities (Clark et al., 2012) and functional traits are any measurable attribute of a species or individual that relates to performance or fitness via impacts on reproduction, growth and survival (Cadotte et al., 2011; Violle et al., 2007). Rather than focusing on taxonomic identity, FD focuses on the mechanisms shaping community composition and, therefore should be more directly related to species responses or effects on ecosystem function and resilience, depending on the functional traits selected for study (Meiners et al., 2015). Since FD does not deal with species identities, which are known to change across ecosystems and spatial scales, it is more easily compared among bioregions. This means that the trait-based approach can also potentially lead to a better understanding of broad patterns in community response to disturbance or stress amongst very different taxa, increasing its appeal as a tool in applied ecology (Cadotte et al., 2011).

Few studies have explored changes in FD across the forest harvest cycle, so far these suggest FD varies depending on the taxonomic group. For instance, Aubin et al. (2013) found that vascular plant FD is relatively unaffected as the stand develops. They and other authors revealed that for arthropods (e.g. carabids, spiders) FD is highest in the early stages of the forest harvest cycle (Aubin et al., 2013; Spake et al., 2016), whereas for birds, Aubin et al. (2013) found that FD increase with forest age. To date, even less research (but see Fountain-Jones et al., 2017) has explored FD in a plantation forest context with a multitaxon approach. This is significant since differences between sylvicultural systems (e.g. tree species, rates of growth and levels of canopy cover) affect environmental filtering meaning that FD may not respond in the same way (Penone et al., 2019).

In this study we take a multitaxon approach to evaluate taxonomic and functional diversity responses through a post-harvest forest chronosequence in two plantation tree species (*Picea sitchensis* (Bong.) Carr. - Sitka spruce and *Pinus sylvestris* L. - Scot's pine) that are expected to exert contrasting intensities of environmental filtering on communities; Sitka spruce is a comparatively faster growing and more shade-bearing tree species than Scots

pine. Four taxonomic groups were chosen for study and these include two autotrophs (vascular plants and mosses) and two arthropod consumers (ground-dwelling spiders and carabids). These taxa are typically abundant within plantations and good ecological knowledge means that reliable trait databases exist for them. We predict the following responses to the environmental filters of stand development:

1) Environmental filtering across the forest harvest cycle exerts similar pressures on taxon and functional diversity so that they respond in the same away
2) A U-shaped relationship between taxon and functional diversity and stand development as a result of declining resources during the middle stages of the cycle, for example reduced light and vegetation cover)
3) Environmental filtering will have stronger influence on species diversity (SD) and FD in Sitka spruce compared to Scots pine because structural changes are more extreme and rapid in Sitka spruce stands.
4) Species with traits favouring tolerance to disturbance will be most common in young plantations.
5) Young plantations are expected to support species with high rates of energy capture dependent on light availability, whereas canopy closure will result in species with traits that indicate tolerance to poor resource availability.

Methods

Experimental design

Forest chronosequences were identified in eight locations throughout Great Britain, in plantations managed by the silvicultural system of clear-cutting and replanting of even-aged, monoculture stands (Figure 2.1). At four of these locations, plantation chronosequences were comprised of Sitka spruce and, at the other four locations, of Scots pine. Each chronosequence encompassed the same four broad stages of the forest harvest cycle and each stage was represented by a forest stand of at least 2.5ha. The four stages included young forest prior to canopy closure (4-21 years in Scot's pine, 7-16 in Sitka spruce), mid-rotation with a closed canopy (28-46 years in Scot's pine, 26-30 in Sitka spruce), commercially mature forest (52-75 years in Scot's pine, 43-49 in Sitka spruce) and over-mature forest with a reopening canopy (84-116 years old in Scot's pine and 81-89 in Sitka spruce). The selected locations represent the optimal planting conditions for each forest type in Great Britain. Sitka spruce is typically planted in upland Great Britain and Scot's pine is planted in both upland and lowland locations. Distances between the four Sitka spruce chronosequences ranged from 65 to 250 km (median: 170km) and between 65km and 750 km (median:620km) for the Scots pine chronosequences. (Figure 2.1). Within chronosequences distances ranged from 0.3-12km for Sitka spruce and 0.2-14km for Scot's pine. Within each chronosequence, the four different stand stages were matched for similar soils, topography, site history, climate and elevation where possible, following criteria used in the Forestry Commission Biodiversity Assessment Project to retain consistency in datasets (Humphrey et al., 2003) (Appendix 2.1). Stands were selected within large forested areas to reduce the influence of non-forested habitat. Within each, a one ha square study plot was established at least 30m from the edge of the stand.

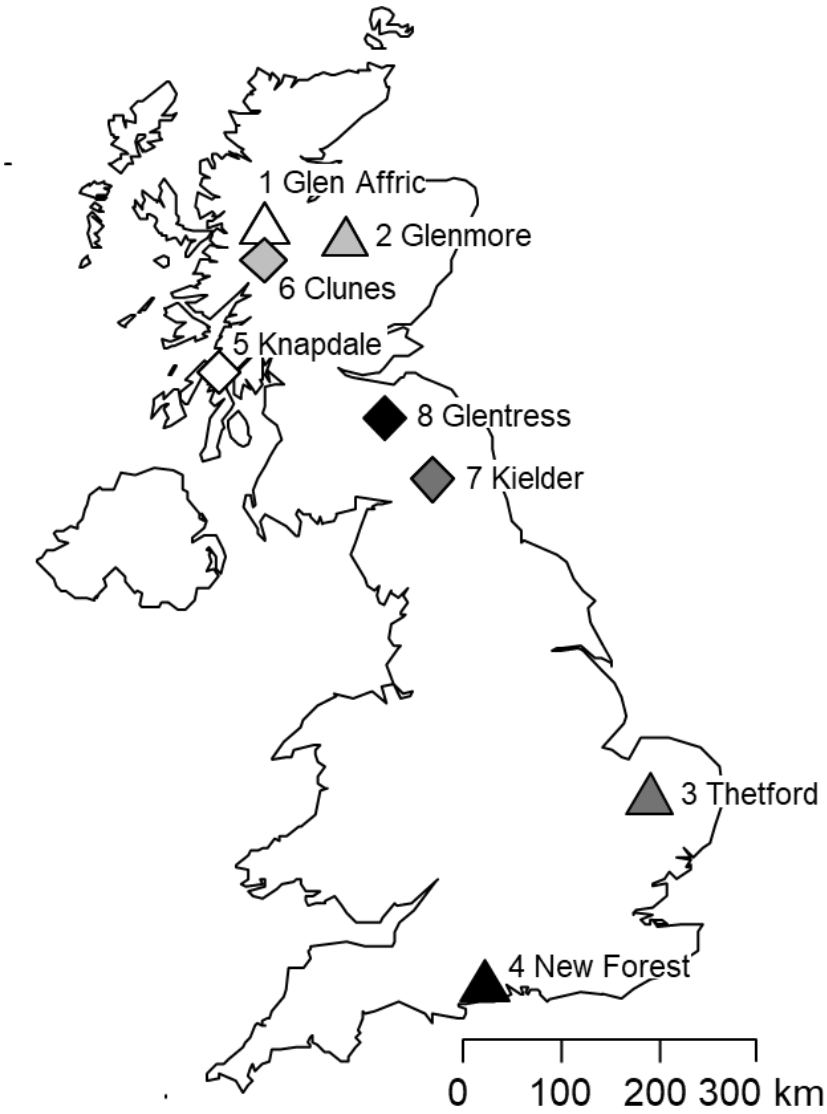


Figure 2.1: Locations of four Scots pine and four Sitka spruce chronosequence clusters across Great Britain. Points are colour-coded by location and tree species. Triangles indicate the locations of Scots pine chronosequences. Diamonds indicate the locations Sitka spruce chronosequences. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent the New Forest. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress. The same colours and shapes are used for each cluster in all relevant figures throughout this chapter.

Data collection

Spider and carabid sampling

Pitfall traps were used to collect ground-active carabid beetles and spiders. Catches are biased towards more active and epigeal carabid and spider species, and so represent relative activity-density of these groups rather than absolute abundance of whole ground-dwelling communities (Thiele, 1977). Six traps were installed in a line running north to south through the centre of each study plot, with traps spaced at 10m intervals (Figure 2.2). Traps

were 75mm in diameter, 110mm deep and contained 50ml of undiluted propylene glycol (antifreeze) as a temporary preservative. A 20cm x 20cm square cover made of galvanised steel was positioned three cm above the ground over the traps to prevent flooding of the traps, debris falling in and to minimise access by small mammals. These lids each had 15cm-wide entrance holes at all four corners which were kept clear of leaf litter and any other debris. As one of the study locations (New Forest) was known to have high densities of potentially disruptive mammals, traps were protected from trampling in all study plots at this location by a cage made from 250x250mm gauge mesh held in place by metal pegs. Neither lids nor mesh cages have been found to affect pitfall trapping efficiency (Siewers et al., 2014). During collections, samples from five traps were pooled and the sixth trap acted as a spare to be used if another trap was interfered with. The traps were run from the beginning of May 2016 for 20 consecutive weeks at each study plot and reset every four weeks. Samples were pooled across the 20 weeks in each plot. All adult carabid beetle and spider species were identified using Luff (2007) and Roberts (1993), respectively.

Vascular plant and moss assessments

Each one ha study plot was split into four 50x50m quarters and each quarter was then split again in half diagonally. Vegetation quadrats measuring 2x2m were placed within each half, resulting in eight quadrats per study plot, spaced at least 15 m apart (Figure 2.2). Percentage cover to the nearest five percent was estimated for all species of vascular plant and moss during June and July 2017. Plot averages were calculated based on these eight quadrats. Keys used to identify mosses and vascular plants included Atherton et al. (2010) and Rose (2006, 1989), respectively.

Environmental characteristics of study plots through a forest harvest cycle

To characterise the environmental changes that occur over the forest harvest cycle, eight 10x10m sub-plots were centred around the eight vegetation quadrats in each study plot to collect a range of primarily stand structural measurements (Figure 2.2). These included tree canopy cover, tree diameter at breast height (DBH), stand density, ground vegetation cover

and needle litter depth. Measured variables were selected based on previous studies in similar settings that show that they evolve substantially over the forest harvest cycle, potentially influencing arthropod and ground vegetation communities (Humphrey et al., 1999; McElhinny et al., 2005; Oxbrough et al., 2005; Purchart et al., 2013; Spake et al., 2016; Ziesche and Roth, 2008).

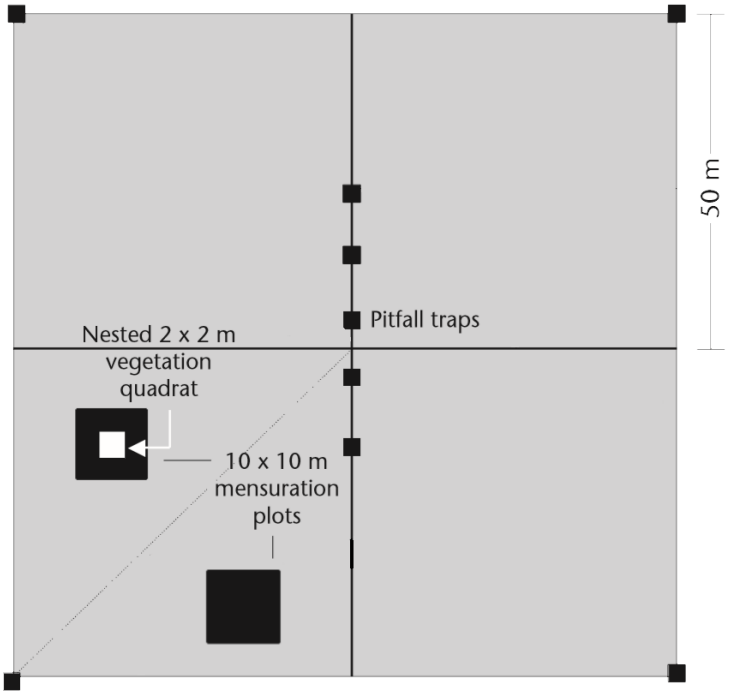


Figure 2.2: Study plot design (mensuration and nested vegetation quadrats were repeated within each 50x50m subplot

Canopy cover was measured four times in the centre of each sub-plot using a spherical densiometer and following manufacturer instructions (Lemmon, 1956). Readings were then averaged for each study plot. The DBH of every tree within sub-plots was measured using a diameter tape to derive a study plot average. Where there were fewer than 10 trees in a sub-plot, the sub-plot size was extended to 20x20m. In pre-thicket study plots, DBH was measured for the first 10 trees above breast-height within eight 5x10m sub-plots. Stand density was measured as the number of stems per ha based on the average number of stems in each sub-plot. Stand basal area is a measure of stand biomass commonly used

by forest practitioners (McElhinny et al., 2005) and was calculated by summing the basal area of all trees in a sub-plot using the following formulae:

$$\text{Basal Area of a tree } (m^2) = (\text{Diameter (cm)}/200)^2 \times \pi$$

$$\text{Stand Basal Area} = (\sum \text{Basal Area of all trees in sub-plot})/\text{area of sub-plot})$$

Stand basal area was averaged across all sub-plots to give a single m^2/ha value per study plot. Since DBH was not measured for all trees in pre-thicket sub-plots, basal area of sub-plots had to be calculated from average DBH instead of the sum of all tree DBH measurements. The following formula was used for this:

$$\text{Stand Basal Area} = (\text{Basal Area of tree with average DBH}) \times (\text{Stand Density/ha})$$

Vegetation percentage cover was estimated to the nearest five percent within each 2x2m vegetation quadrat at the centre of each sub-plot. Needle litter depth was measured at four random points within each sub-plot from the forest floor surface to the fermentation layer (i.e. where litter was decomposing and was no longer identifiable as needles).

Functional trait selection

Functional response traits were selected to reflect a taxon's ability to respond and/or adapt to the major environmental filters expected to be present during a post-harvest chronosequence (i.e. changing light levels due to changes in stand structure). Three traits were selected for each of the taxonomic groups related to dispersal ability, resource acquisition and size (Table 2.1). Only these traits were chosen in order to reduce correlation whilst maximising the variance explained. In addition, for spiders and carabids, these represent the only reliable and available traits, since the functional roles and responses of these taxa are much less understood than vascular plants and mosses. Sources of trait information for each taxonomic group was as follows: carabids (Carabids.org - Homburg et al., 2014; Luff, 2007), spiders (Bell et al., 2005; Cardoso et al., 2011; Araneae:Spiders of

Europe - Nentwig et al., 2019), vascular plants (LEDA –Kleyer et al., 2008), mosses (BRYOATT - Hill et al., 2007).

Table 2.1: Functional traits selected for each taxonomic group with information on trait values, rationale for selection and supporting literature

Taxa	Trait	Levels	Rationale	Literature
Vascular plant	Canopy height	Continuous (m)	Height is related to competitive ability, with the tallest plants having greatest access to light resources.	Douma et al., 2012 Kleyer et al., 2008 Westoby, 1998
	Seed mass	Continuous (mg)	Indicates dispersal and reproductive effort and is an adaptation to disturbance. Smaller seeds are more numerous and disperse over longer distances, improving dispersal ability and increasing the chances of finding suitable habitat. Plants with larger seeds survive better in sub-optimal conditions.	Douma et al., 2012 Kleyer et al., 2008 Westoby, 1998
	Specific Leaf Area (SLA)	Continuous (mm^2/mg)	Represents the rate of return on investment in photosynthesis and is related to responsiveness to opportunities for growth. Low SLA indicates a slow-growing, less competitive species and high SLA allows a flexible and fast response to resource availability and higher competitive ability.	Kleyer et al., 2008 Vendramini et al., 2002 Westoby, 1998
Moss	Shoot length	Continuous (mm)	Related to competitive ability/ability to tolerate stress. Large species are better competitors in favourable conditions whereas small species are better stress-tolerators	Boudreault et al., 2018; Virtanen, 2014
	Spore size	Continuous (µm)	Related to dispersal/reproductive effort. Smaller spores are expected to be more numerous and disperse over longer distances, improving dispersal ability and increasing the chances of finding suitable habitat	Caners et al., 2013; Lönnell, 2014; Virtanen, 2014
	Life-form	Turf Weft Mat	Refers to the organisation of shoots into colonies and has consequences for resisting stresses (especially low water). Wefts and turfs are better adapted to prevent water loss than mats, thus allowing them to persist in a post-disturbance environment.	Bates, 1998; Birse, 1957; Caners et al., 2013
Carabid	Size	Continuous (cm)	The reproductive rate of smaller species tends to be greater than larger species and their life cycle shorter. The greater fecundity and a shorter time period required for maturation favours the rapid establishment of smaller carabid species in recently disturbed areas.	Blake et al., 1994; Kotze and O'hara, 2003; Mullen et al., 2008; Thiele, 1977
	Diet	Specialist predator Generalist predator Herbivore Omnivore	Represents resource-use. Herbivorous species are directly dependent on plant species richness and cover, whereas generalist predators and omnivores have a broader diet and increased likelihood of successfully finding food in a resource- poor environment.	Aubin et al., 2013; Hunter and Price, 1992; Thiele, 1977
	Wing-form	Winged Wingless Wing-dimorphic	Relates to dispersal ability. Winged carabids have better dispersal ability and are expected to be less vulnerable to disturbance events or unsuitable habitat.	den Boer, 1990; Mullen et al., 2008; Niemelä, 2001
Spider	Size	Continuous (mm)	Relates to competitive ability, ability to tolerate stress and dispersal over short distances. Large spiders have a competitive advantage under mutual predation, can travel faster due to proportionally longer legs and are better adapted to variations in microclimate than smaller spiders	Aubin et al., 2013; Eichenberger et al., 2009; Foelix, 1983
	Ballooning	Yes No	Represents dispersal ability. Ballooning spiders have better dispersal ability and are expected to be less vulnerable to disturbance vents or unsuitable habitat.	Aubin et al., 2013; Entling et al., 2011
	Hunting method	Ambush Orb-web Space-web Running Sheet-web	Microclimate determines the level of activity of active hunters, particularly running hunters; the warmer the conditions, the higher the level of activity. All web--builders require anchor points for their webs and structurally complex vegetation is required in particular by orb and space-web weavers.	Aubin et al., 2013; Cardoso et al., 2011; Košulič et al., 2016; Michalko and Pekár, 2016

Data analysis

Data Preparation

Where there was zero total abundance of any given taxa in a study plot for the duration of the sampling period, these samples were excluded from the dataset. This included carabid beetles from one mid-rotation spruce plot and vascular plants from another mid-rotation spruce plot. To account for any difference in trap days between study plots, the abundance of each species in each plot was divided by the actual number of trap days and multiplied by the maximum number of trap days. Trap days at all sites varied from 139-140 except for one site which, due to logistical reasons, was only sampled for 85 days.

For all analyses, age in years rather than stand stage was used as the explanatory variable representing change across the forest harvest cycle. Using a continuous variable rather than a categorical variable increased the power of analysis and removed biases caused by the arbitrary categorisation of stand age.

Diversity indices and traits

Simpson's index of species diversity was used as a measure of SD (Simpson, 1949) and Rao's quadratic entropy index (Rao, 1982) was used as a measure of FD (Rao, 1982). SD was chosen because it accounts for relative abundance and number of species. FD is a measure of the abundance-weighted sum of dissimilarity between species and was chosen because it is typically more independent from the number of species in a community than other functional diversity indices (Botta-Dukát, 2005). Independence from species richness is important in this case because communities were likely to have been sampled from different species pools, given the geographic spread of the study plots. It is not possible to calculate FD for communities with fewer species than the number of functional traits (in this case, fewer than three). This occurred with the carabid and vascular plant data in three spruce plots. FD was assumed to be 0 for these study plots.

Community Weighted Means (CWM) of each trait were calculated as a measure of functional composition for each taxon and forest type separately using the traits listed in Table 2.1. For continuous traits, CWMs represent the average trait value in a community weighted by the relative abundance of each species. For categorical variables, this calculates the proportion of individuals with each possible trait value per community.

Species with missing trait information were removed only if they occurred infrequently i.e. two carabid species (one individual and two individuals, respectively) were removed. Tree species, even if they occurred only as seedlings and saplings in quadrats, were removed from vascular plant datasets since the comparatively large canopy height achieved by these species at maturity was expected to skew results for this group. Tree species removed included two species in spruce stands and five species in pine stands which contributed 6.5% and 10% to total percentage cover in each forest type, respectively.

Models

To determine how SD, FD and functional composition (CWM) respond to environmental changes within each crop type, general additive mixed modelling (GAMM) was carried out for each trait (continuous), or trait level (categorical), FD and SD. GAMM was used because relationships between response and explanatory variables were predicted to be non-linear. Chronosequence location was included as a random factor. When location was not significant, this was removed from the model except when this reduced the variation explained. Models were checked for normal distribution of residuals and homoscedasticity before proceeding. Finally, Benjamini and Hochberg corrections were applied to p values to minimise Type I errors. This correction is less conservative than other methods and so also reduces the risk of Type II errors.

For both spiders and carabids, categorical traits were typically dominated by one or two trait values and so CWM values for the remaining trait values were consistently close to zero. Modelling was attempted for these trait values but, due to a lack of data, it was not possible

to fit acceptable models. This included herbivorous, omnivorous and wing-dimorphic carabids and ambush hunting, orb-web weaving and sheet-web weaving spiders in pine and spruce, as well as running hunting spiders in spruce (see Appendix 2.4 tables e and f for a summary of cwm values for these traits).

All analyses were carried out in R (R Core Team, 2019). The “melodic” function was used to calculate abundance-weighted FD and SD using a distance matrix created using the “trova” function (de Bello et al., 2016; De Bello et al., 2013). CWMs were calculated using the “functcomp” function of the FD package (Laliberté et al., 2014; Laliberte and Legendre, 2010). All models were fit using the “gam” function of the mgcv package (Wood, 2015, 2011).

Results

Overview

59 species of vascular plant and 27 species of moss were identified across all pine study plots. In spruce study plots, 37 species of vascular plant and 24 species of moss were identified. 1593 adult carabids belonging to 35 species were identified in Scots pine plots and 986 individuals from 25 species in Sitka spruce. 2033 adult spiders belonging to 91 species were identified in the Scots pine plots and 1766 adult spiders belonging to 68 species in the Sitka spruce plots. See Appendix 2.3 for a summary of species identified for all taxonomic groups in Sitka spruce and Scots pine at different stages of the forest harvest cycle. See Appendix 2.4 for a summary of SD, FD and CWM for all taxonomic groups in Sitka spruce and Scots pine.

Environmental characteristics of study plots through a forest harvest cycle

Basal area increased linearly through the forest harvest cycle in both pine and spruce (Figure 2.3), however in spruce it reached a plateau at commercial maturity, whereas for pine, basal area continued to increase. Similarly, DBH increased linearly with age for both forest types, with no plateau reached. Stand density was highest in the earliest stages of the forest harvest cycle and was greater in Sitka spruce compared with Scots pine at this stage. Stand density subsequently declined in both forest types to reach a comparable level, although the decline was steeper in spruce stands. There was a steep linear increase in canopy cover, leading to a plateau at around 30 years into the forest harvest cycle in the spruce and pine study plots. Canopy cover at this plateau was marginally higher in spruce compared to pine. Vegetation cover decreased rapidly in the spruce study plots with falling light levels, reaching its lowest level at commercial maturity. This was reflected by a shallower decline in the depth of the litter layer. Subsequently vegetation and litter depth recovered to reach similar levels at 90 years as the youngest stands sampled. Vegetation

cover and litter depth remained the same throughout the pine forest harvest cycle. See Appendix 2.2 for average values of all environmental variables in each study plot.

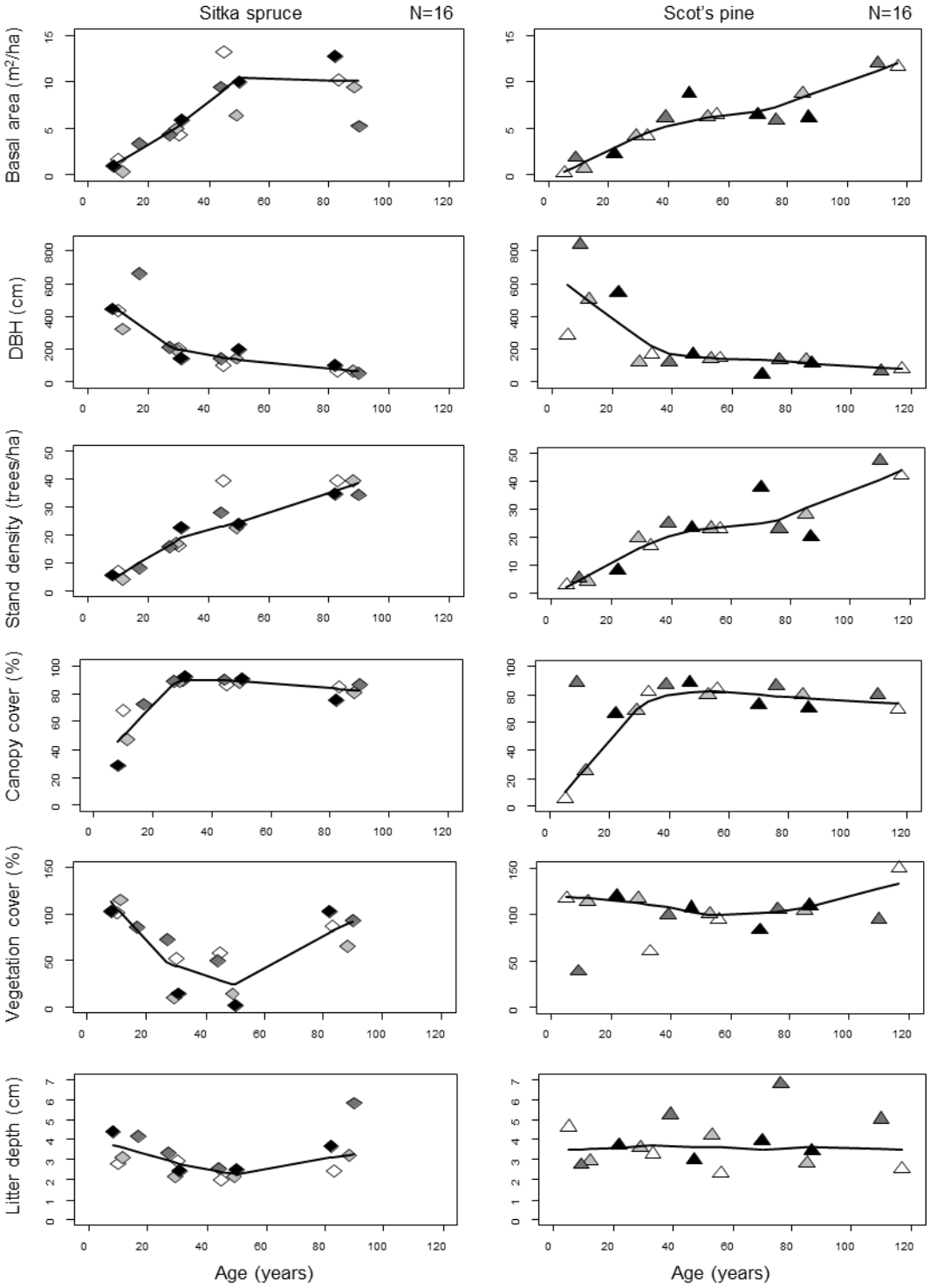


Figure 2.3: The relationship between stand structure variables and stand age in Sitka spruce and Scots pine study plots. Lines were fitted with a lowess function. Colour represents chronosequence location. In spruce, white circles represent Knapdale, light grey circles represent Clunes, dark grey circles represent Kielder and black circles represent Glentress study plots. In pine, white circles represent Glen Affric, light grey circles represent Glenmore, dark grey circles represent Thetford and black circles represent New Forest study plots.

Taxonomic and functional diversity through the forest harvest cycle

Trends in SD were similar to those of FD across taxa and forest types, although most did not change significantly through the forest harvest cycle (Figure 2.4). Where they changed significantly, only a few exhibited the expected U-shaped response.

In pine, neither SD nor FD of any taxon changed significantly through the forest harvest cycle. Moss FD however, had a weak trend ($p=0.1$) for decline with stand age until around 80 years. Spider SD showed a weak U-shaped trend ($p=0.06$) with stand age, with a turning point at around 70 years.

In spruce forests, vascular plant SD decreased significantly with forest age, while FD showed no significant relationship. Moss SD, on the other hand, did not change significantly but FD had a weakly positive trend ($p=0.06$) with stand age after around 50 years. Carabid SD and FD had a U-shaped trend with stand age, with a turning point at 30 years. This trend was only significant for FD and near-significant for carabid SD ($p=0.1$). There was a U-shaped trend in spider SD and FD with stand age, with a turning point at around 50 years. However, this trend was only significant for spider FD and not for SD ($p=0.17$). See Appendix 2.5, Tables a and b for summary statistics of all SD and FD models.

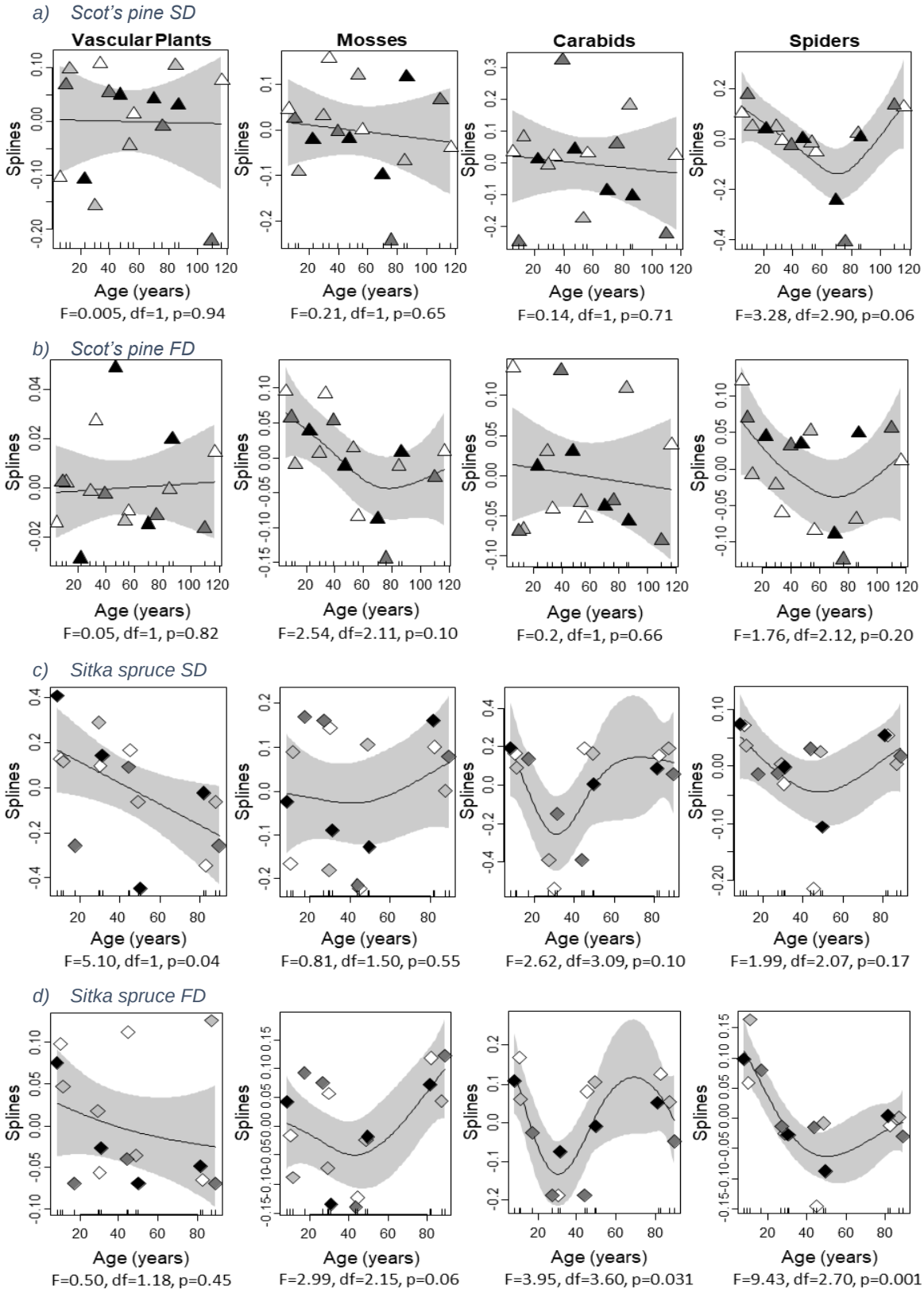


Figure 2.4: GAMM plots showing the relationship between stand age and a) species diversity and b) functional diversity for each taxon in Scot's pine stands and c) species diversity and d) functional diversity for each taxon in Sitka spruce stands. Y axes represent SD and FD and values are centred around zero. Model predictions, standard error intervals, p values, F statistic values and estimated degrees freedom of are shown. Predictions are colour-coded by location. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent New Forest study plots. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress study plots.

Functional traits of communities through the forest harvest cycle

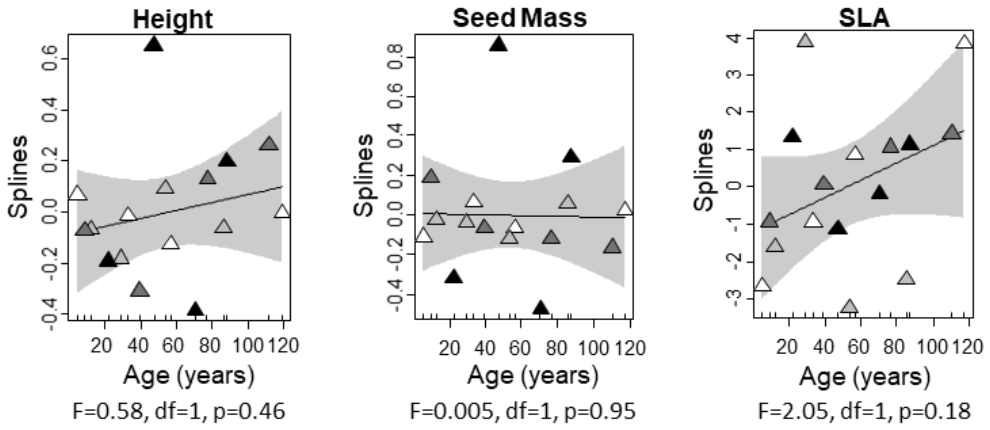
Vascular plant seed mass, plant height and SLA showed no significant changes through the pine or spruce forest harvest cycles (Figure 2.5). In pine forests, moss spore size and moss length did not change significantly through the forest harvest cycle but there was a weak linear decline ($p=0.08$) in the proportion of mat-forming mosses and a significant increase in weft-forming mosses with age. However, these were not significant after benjamini and hochberg corrections. The proportion of turf-forming mosses did not change with pine stand age. In spruce, moss spore size had a significant positive linear relationship with age, but this was not significant after corrections. There was a significant U-shaped trend in moss length with a turning point at 50 years into the spruce harvest cycle. Tuft-forming mosses had a significant U-shaped response to the spruce harvest cycle with a turning point at 50 years. The proportion of other moss life-forms did not change significantly during the spruce forest harvest cycle (Figure 2.6).

No carabid traits responded significantly to stand age in pine or spruce forests, except carabid size in Sitka spruce which increased significantly from around 40 years into the forest harvest cycle (Figure 2.7). However, this was no longer significant after corrections. Spider ballooning behaviour, size and hunting guild did not respond significantly to the forest harvest cycle in pine forests, but space web-weavers showed a weak negative trend with age ($p=0.07$). Ballooning behaviour in spruce forests showed no significant change through the forest harvest cycle. Spider size significantly and steeply declined until 30 years into the spruce harvest cycle. The proportion of sheet-web weavers in spruce forests increased steeply and significantly until about 40 years and space-web weavers showed the opposite trend, decreasing significantly until about 40 years into the forest harvest cycle (Figure 2.8). The trend for space-web weavers was not significant after corrections

Wing-dimorphic, herbivorous and omnivorous carabids were too rare in both forest types to model reliably and were not tested, as were running hunting spiders in spruce and ambush

hunting and orb-web weaving spiders in both forest types. See Appendix 2.5 Tables c for summary statistics of all CWM models

a) *Scot's pine*



b) *Sitka spruce*

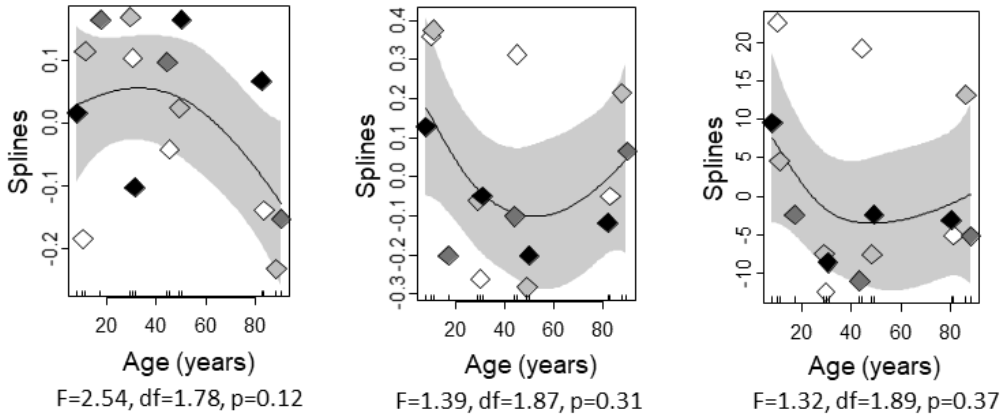
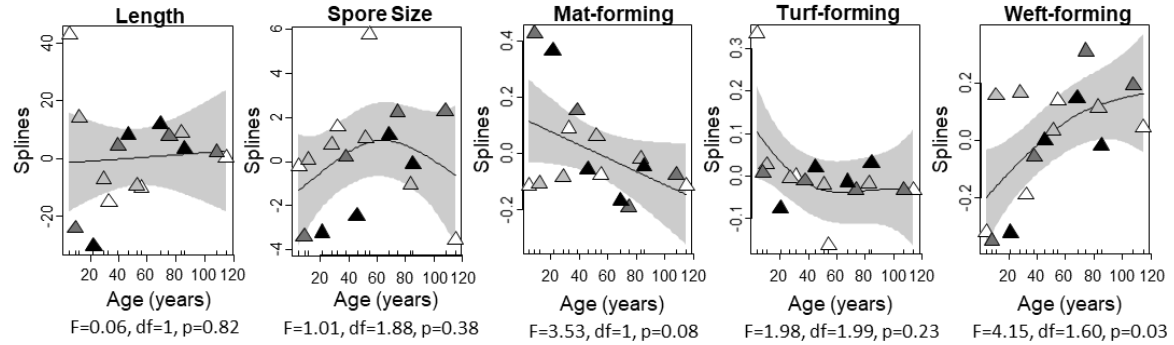


Figure 2.5: GAMM plots showing the relationship between age and vascular plant trait CWMs in (a) Scot's pine and (b) Sitka spruce stands. Y axes represent (from left to right) average plant height, average seed mass and average SLA and values are centred around zero. Model predictions, standard error intervals and p values are shown. Significant p values after benjamini and hochberg correction are shown in bold. Predictions are colour-coded by location. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent New Forest study plots. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress study plots.

a) *Scot's pine*



b) *Sitka spruce*

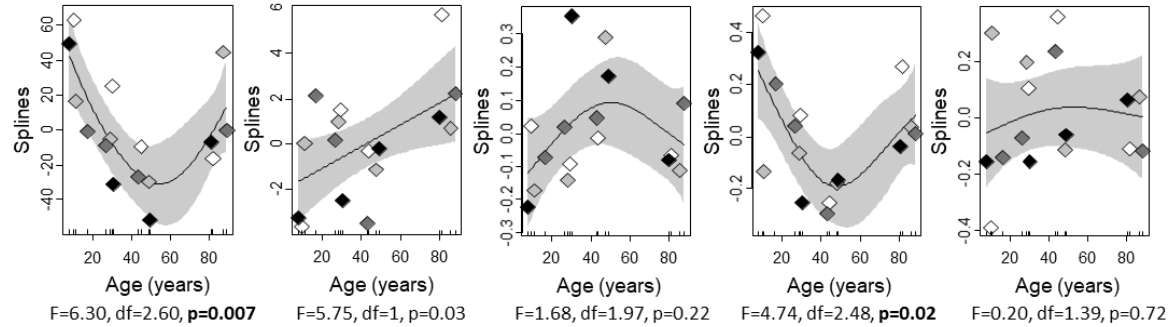
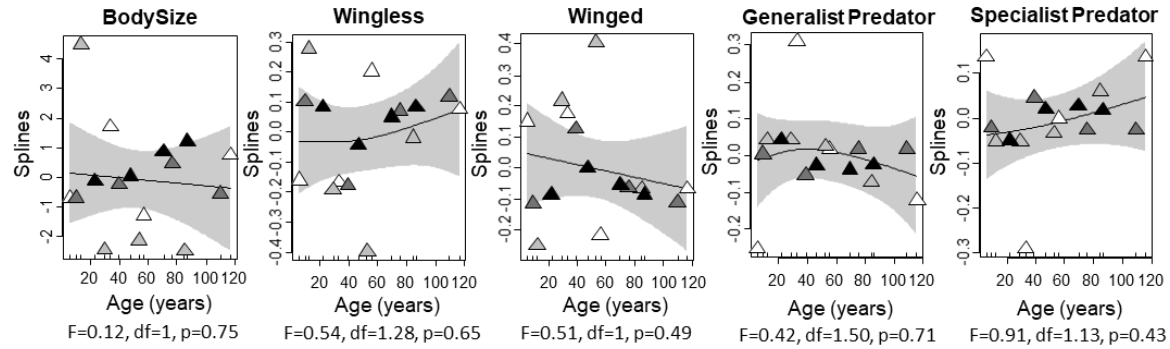


Figure 2.6: GAMM plots showing the relationship between age and moss trait CWMs in (a) Scot's pine and (b) Sitka spruce stands. Y axes represent (from left to right) average moss shoot length, average moss spore size and proportion of individuals and values are centred around zero. Model predictions, standard error intervals and p values are shown. Significant p values after benjamini and hochberg correction are shown in bold. Predictions are colour-coded by location. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent New Forest study plots. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress study plots.

a) *Scot's pine*



b) *Sitka spruce*

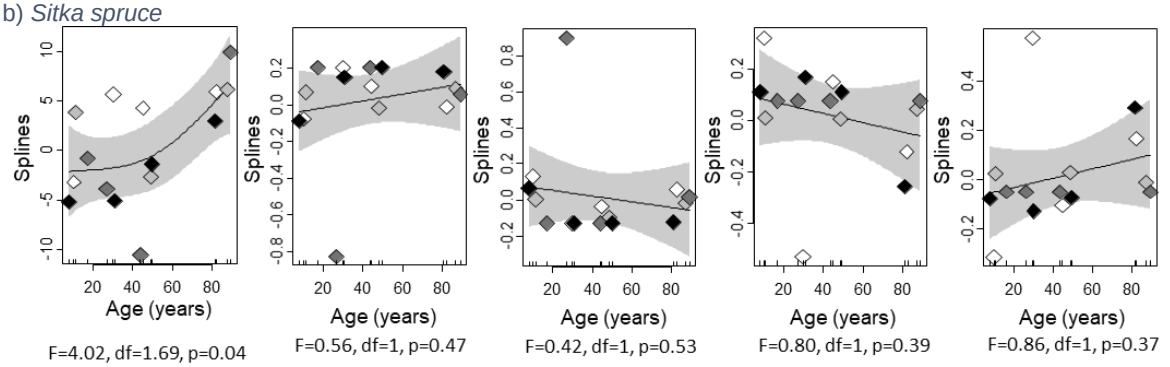
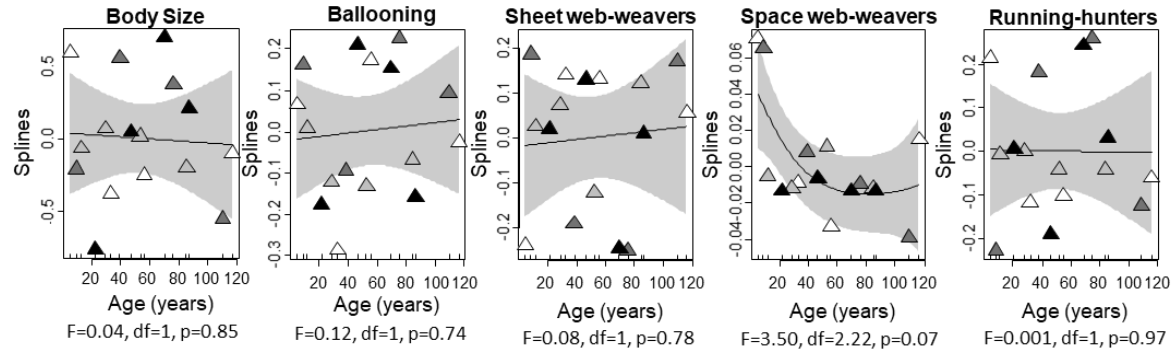


Figure 2.7: GAMM plots showing the relationship between age and carabid functional trait CWMs in a) Scots pine and b) Sitka spruce stands. Y axes represent (from left to right) average carabid body size and proportion of individuals. Y axis values are centred around zero. Model predictions, standard error intervals and p values are shown. Significant p values after benjamini and hochberg correction are shown in bold. Predictions are colour-coded by location. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent New Forest study plots. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress study plots.

a) *Scot's pine*



b) *Sitka spruce*

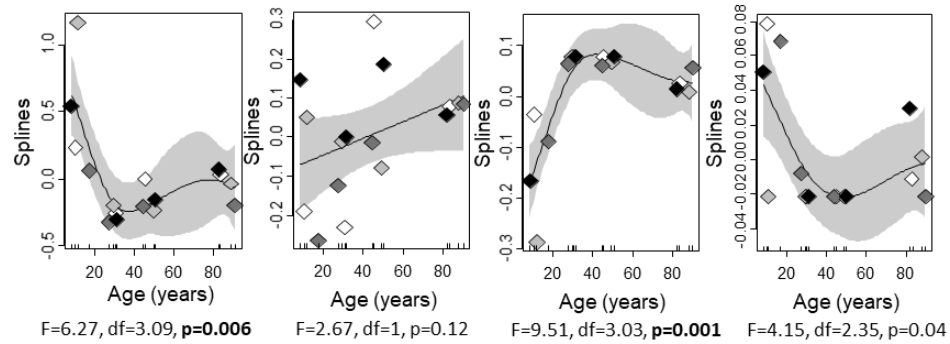


Figure 2.8: GAMM plots showing the relationship between age and spider functional trait CWMs in a) Scots pine and b) Sitka spruce stands. Y axes represent (from left to right) average spider body size and proportion of individuals. Y axis values are centred around zero. Model predictions, standard error intervals and p values are shown. Significant p values after benjamini and hochberg correction are shown in bold. Predictions are colour-coded by location. In pine, white triangles represent Glen Affric, light grey triangles represent Glenmore, dark grey triangles represent Thetford and black triangles represent New Forest study plots. In spruce, white diamonds represent Knapdale, light grey diamonds represent Clunes, dark grey diamonds represent Kielder and black diamonds represent Glentress study plots.

Discussion

Overall, we found broadly similar responses in SD and FD across taxa. This was expected since species survival depends on how well suited their functional response traits are to environmental conditions, and this usually leads to a synchronised response (Olden and Rooney, 2006). However, SD and FD were not always both significant for a taxon group. For example, carabid and spider SD and FD showed very similar trends across the spruce forest harvest cycle, but these were only significant for FD, indicating more subtle effects in SD. This could be an indication that changes in ecosystem functioning are occurring despite few changes in SD (De Bello et al., 2010). On the other hand, we found evidence of a stronger effect on SD for vascular plants in spruce forests. This can indicate a loss of functional redundancy and therefore a loss of resilience in communities (Cadotte et al., 2011). Similarly, Aubin et al. (2013) found that different diversity metrics, including functional and taxonomic diversity, do not always respond in the same way or with the same strength to forest succession. Although differences between SD and FD were subtle, they may indicate important changes in these communities and illustrate the value of considering a variety of metrics of diversity in order to enhance the understanding of causes and consequences of environmental changes.

We predicted a U-shaped response for both SD and FD with age because canopy development increasingly limits light availability at the forest floor in the mid stages of the forest harvest cycle after which tree thinning begins to reopen the canopy (Penone et al., 2019). However, we found few such responses and, where trends were U-shaped, most were not significant. Instead, no significant changes were found in Scots pine across the forest harvest cycle for SD and FD in any taxon group, whereas responses varied by taxon group in Sitka spruce. Yet, this does suggest that our prediction that environmental filtering would be stronger in Sitka spruce as compared to Scots pine was accurate, even if the response in Sitka spruce was not U-shaped. This difference in response may be driven by the observed faster rate of and more complete canopy closure during spruce stand

development which results in a near-complete loss of forest-floor vegetation. This, in turn, influences the diversity and abundance of primary consumers and their predators (Russell, 1989). As spruce stands approach commercial maturity, self-thinning processes or thinning management begin to reopen the canopy and vegetation cover begins to increase again. Scot's pine is known to have a sparser canopy compared to Sitka spruce and so does not shade out understorey vegetation to the same extent (Hale et al., 2009). As far as the authors are aware, there are no studies comparing diversity across full chronosequences of commercial plantations with different dominant tree species in the same regions nor exploring diversity across the length of a Scots pine plantation forest harvest cycle to compare with these results.

SD and FD of vascular plants and the composition of their traits did not change throughout pine or spruce harvest cycles, providing little evidence of environmental filtering effects, except for SD in spruce forests which decreased with stand age. Vascular plant species and FD have shown no response to stand development in similar studies (Aubin et al., 2013; Curzon et al., 2017) whereas functional traits have been found to be responsive to changes in forest structure (Aubin et al., 2013; Curzon et al., 2017; Sabatini et al., 2014). These changes in forest floor vascular plant traits are said to be driven by overstorey disturbance and development. Aubin et al. (2013) noted that plant communities returned to pre-disturbance composition very quickly, with some traits changing within five years of harvesting. Further, Hilmers et al. (2018) found a U-shaped trend in the number of vascular plant species along a forest succession which was driven by increased abundance of plants in early successional stages and very old forests due to increased light levels. Early successional plantation forest stands, immediately after the large disturbance of clear-fell harvesting, often have greater vascular plant diversity (Aubin et al., 2013; Bartha et al., 2008; Eycott et al., 2006) whereas old forests have more time to develop old-growth features and develop a higher diversity of vascular plants (Hilmers et al. 2018). We did not sample these extremes in ages, so may not have been able to detect all changes to vascular

plant communities in our study. However, the more extreme changes observed in Sitka spruce stand development allowed us to detect a decline in vascular plant SD.

Unlike vascular plants, moss functional traits did respond to changes in the spruce harvest cycle, though there was little change in these throughout the pine harvest cycle. Since moss shoot length has been linked to competitive ability under optimal conditions (Löbel et al., 2018; Virtanen, 2014), larger shoot length in the youngest and oldest spruce stands suggests that there may be better availability of resources such as light and water at these stages of spruce harvest cycles. This may explain the U-shaped trend we found in spruce for this trait. Further, mosses compete with vascular plants and so the higher vegetation cover at the beginning and end of the spruce harvest cycle that we found, may select for more competitive mosses too also driving this trend in our data (Grime and Pierce, 2012; Jonsson et al., 2015). In contrast, in the more open pine forest, competition from vascular plants throughout the forest harvest cycle could explain why moss shoot length did not change with stand age.

Changes in moss life-forms would suggest that water availability was sub-optimal at the beginning and end of the spruce forest harvest cycle since this is where we found water stress-tolerant turf-forming mosses were most common (Birse, 1957). Indeed, it is understood that maturing spruce stands, with almost complete canopy closure, provide a more sheltered, humid and stable microclimate than earlier or later in the forest harvest cycle (Hale et al., 2009; Humphrey et al., 2003; Penone et al., 2019). It is unclear, however, why weft and mat-forming mosses, the other moss life-forms recorded from these forests, did not respond to stand age since water stress is also expected to influence their distribution (Birse, 1957). However, other studies have also found that wefts in particular are not affected by changing canopy cover (Caners et al., 2013). This functional trait could also be related to factors other than water stress such as competitive ability (Bates, 1998) or trade-off with nutrient absorption (Proctor et al., 2007). In addition, moss life-form has also demonstrated plasticity, and so may not be accurately measured by species-based

trait databases as opposed to individual-based measurements (Bates, 1998). Optimal light availability in young and old spruce stands and optimal water availability during the middle stages of the spruce forest harvest cycle, may explain why there was no change in moss diversity. While some studies have found that bryophyte diversity is positively correlated with light availability at the forest floor (Hilmers et al., 2018; Raabe et al., 2010), this does vary with bryophyte substrate and also with how well local climates buffer water balance (Bartels et al., 2019; Proctor et al., 2007). For example, in a study of stream-side boreal forests, bryophytes species richness did not respond to clear-felling (Dynesius and Hylander, 2007). This suggests that cooler or more humid climates can buffer changes in microclimate due to changes in canopy cover.

Moss spores were expected to become larger as the forest harvest cycle progressed, but no changes were found in spruce or pine forests. Further, all mosses sampled in both forest types had spores below a proposed threshold of 20µm, above which mosses are not likely to be easily wind-dispersed (Löbel et al., 2018). This indicates strong dispersal ability throughout the forest harvest cycle in both forest types. Further, mosses restricted to old-growth or natural forests often have much larger spores (e.g. 310µm) in order to survive periods of stress while resources or substrates such as deadwood are unavailable (Löbel et al., 2018), suggesting that none of the mosses sampled here were true forest specialists. The lack of observed gradient may also be due to the absence of very young or very old plantation stands in our chronosequences.

Carabid and spider diversity demonstrated approximately U-shaped relationships with stand age in spruce forests, although this was not significant in all cases. This result is supported by other studies of similarly aged forests and ground vegetation and canopy cover are often suggested to be driving these changes (Butterfield, 1997; Mullen et al., 2008; Niemelä et al., 1996; Spake et al., 2016; Taboada et al., 2008). The presence of predatory carabids and spiders is linked to ground vegetation diversity and structure since these influence herbivorous prey and microclimate and provide shelter as well as web

anchor points for spiders (Bultman and Uetz, 1982; Roberts, 1993; Russell, 1989; Uetz, 1991). Since ground vegetation cover decreased during the first half of the spruce harvest cycle, spider and carabid diversity also declined. Additionally, since ground vegetation changed less through the pine forest harvest cycle, diversity of both carabids and spiders was also less affected.

Although both spider and carabid diversity show evidence of increasing again in spruce forests, this appears to be happening at different rates for each taxon. Spiders in particular are strongly affected by the structural complexity of vegetation (Halaj et al., 1998; Scheidler, 1990). Although vegetation structure was not directly measured in this study, it was observed during data collection that the oldest stands contained mostly grasses and forbs compared to the more ericaceous shrub communities of the youngest stands. The structural complexity of these plant communities is very different, with ericaceous shrubs potentially providing more anchor points for a wider diversity of spider hunting guilds, and this could explain why spider FD had not increased more in the oldest spruce stands. Changes in spider hunting guilds in spruce forests support this hypothesis since only one hunting guild, sheet-web weavers, almost completely dominated spider communities after around 30 years into the spruce forest harvest cycle. Sheet web-weavers may survive in these structurally simple, low resource stands because they are thought to be more dependent on a cool, moist climate and low competition and predation than they are on food availability (Kumschick et al., 2009). Additionally, although most other hunting guilds were too infrequent to formally analyse, actively hunting spiders almost exclusively occurred in the youngest spruce stands, as did many other web-weaving guilds.

As well as effects on vegetation, lower canopy cover can lead to warmer microclimates (Ferrez et al., 2011), which we would expect in all of our Scot's pine forests and the young Sitka spruce forests. This higher solar radiation favours greater activity of epigeal arthropods such as spiders and carabids (Høye and Forchhammer, 2008). Further, these conditions are said to support energetically expensive forms of prey capture with higher

rates of failure such as active-hunting. Where resources are more limited, a strategy that requires less energy and has a lower failure rate, such as web-weaving, is considered a safer strategy (Grime and Pierce, 2012). Other studies have found running-hunting spiders to be most common in young, open stands and highly disturbed habitats and these are then replaced by web-building species, particularly in older, stable forest stands (Aubin et al., 2013; Pedley and Dolman, 2014). This reflects the results found in spruce stands in this study but not pine and may be due to the sparser canopy of Scot's pine throughout the forest harvest cycle. Changes in spider size during the spruce forest harvest cycle, and the dominance of ballooning behaviour may be an artefact of the dominance of sheet-web weavers in all forests, but especially spruce forests. This guild consists of the typically small Linyphiid spiders, many of which are thought to be capable of ballooning. However, the decreasing trend in spider size is consistent of the findings of other studies (Aubin et al., 2013; Pedley and Dolman, 2014). Large body size is considered to be advantageous in exposed, open habitats where conditions are likely to fluctuate more extremely, such as in young forest stands (Entling et al., 2010).

No significant changes in any carabid functional traits were detected suggesting that size, diet and wing-form are unrelated to forest age in our plantations. Various studies suggest that large, wingless carabids are more common in long-term stable habitats and so body size was expected to increase and dispersal ability decrease with stand age (Homburg et al., 2013; Pedley and Dolman, 2014; Ribera et al., 2001). As previously identified, this study may not have sampled early enough in the forest harvest cycle to observe significant shifts in these functional traits of carabids, considering turning points in many carabid functional traits appear to occur before 10 years into the forest harvest cycle (Aubin et al., 2013).

Conclusions

In some cases, taxonomic groups responded in different ways to environmental filtering during the progression of the forest harvest cycle, highlighting the importance of including multiple taxa in studies of this kind. Despite these inconsistencies, some overall conclusions

can be made in terms of the impact of plantation forest harvest cycles on multiple taxa. SD and FD in pine forests was, broadly speaking, similar throughout the forest harvest cycle. However, SD and FD in spruce forests declined for some groups from around 30 years into the forest harvest cycle. This is evidence of the predicted U-shaped relationship between diversity and stand age and indicates that mid-rotation spruce stands are less diverse and therefore may be less resilient to future perturbations, particularly in comparison to younger stands (Gunderson, 2000; Oliver et al., 2015). A different approach to the management of these stands may need to be considered since a target of plantation management is the "maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems" (Forestry Commission, 2017; Standing Forestry Committee, 2015). Given that canopy cover is such an important factor in determining the diversity of multiple taxonomic groups in plantation forests, management approaches that result in a more open canopy may improve the ability of spruce plantations to support SD and FD. On the other hand, this study indicates that pine forests may be equally resilient at all stages of the forest harvest cycle.

This study included forest stands that were over-mature (e.g. those not felled at commercial maturity). These aim to improve provision of ecosystem services such as recreation and to support biodiversity. All taxa in pine forests showed similar SD and FD, as well as functional trait composition throughout the forest harvest cycle and so there is no evidence that over-mature stands of this forest type contribute uniquely to biodiversity. There was evidence that diversity in over-mature spruce stands had begun to increase beyond that of maturing stands for taxa which experienced declining diversity with stand age. The over-mature stands sampled here, at roughly 100 years old, are still young relative to ecologically mature forests, where trees can be several hundred years old. Since older stands were not sampled, and could not be sampled for Sitka spruce since these do not exist in Great Britain, it remains to be seen whether over-mature stands could develop stand characteristics that support higher diversity compared to maturing plantations. This is especially true for moss

communities in Sitka spruce forests, where over-mature stands appeared to support the most functionally diverse moss communities.

The trait values of most taxonomic groups did not respond as predicted to the forest harvest cycle. The inclusion of a greater range of stand ages may have resulted in the U-shaped curve that was predicted and that has been found in similar studies with longer forest succession gradients (Aubin et al., 2013; Hilmers et al., 2018). In addition, measurement of individual-based trait values, or intraspecific trait variation, may have revealed trait responses that species-based trait values from trait databases did not (Albert et al., 2011). Furthermore, functional traits revealed, in some cases, that the communities sampled did not hold trait values expected of typical forest communities. For example, spider and moss communities at all stages in both pine and spruce forest harvest cycles appeared to be well adapted for dispersal. Since predictions assumed that forest specialists would colonise plantations stands as they aged, the lack of forest specialists may explain why these predictions were not accurate. To put these results in to context, it would be valuable to establish what a typical forest specialist community should look like in Great Britain.

Chapter 2 Appendices

Appendix 2.1: Locations and characteristics of pre-thicket (PT), mid-rotation (MR), mature (M) and over-mature (OM) Scots pine and Sitka spruce study plots.

Location	Study plot number	Stand stage	Age at sampling	% of main crop species	Rotation	Previous land use	Study plot locations Lat	Long	Plot elevation (m.a.s.l.)
Scot's pine									
Glen	1.5	PT	4	100	2	Native pinewood	57.2612	-4.8776	240
Affric	1.1	MR	32	94	1	Heath/grassland	57.3468	-4.7209	200
	1.2	M	55	95	1	Heath/grassland	57.2928	-4.8577	300
	1.3	OM	116	95	1	Native pinewood	57.2701	-4.8663	190
Glenmore	2.6	PT	11	70	2+	Native pinewood	57.1534	-3.7043	400
	2.5	MR	28	70	1	Native pinewood	57.1524	-3.7061	400
	2.2	M	52	81	1	Native pinewood	57.1938	-3.7512	380
	2.3	OM	84	90	1	Native pinewood	57.1697	-3.6743	430
Thetford	3.3	PT	8	63	2	Heath/grassland	52.4293	0.6849	60
	3.1	MR	38	100	1	Heath/grassland	52.4749	0.7006	30
	3.5	M	75	80	1	Heath/grassland	52.4702	0.7160	50
	3.6	OM	109	100	1	Heath/grassland	52.4252	0.6335	20
New	4.5	PT	21	100	2+	Native oakwood	50.8449	-1.6847	50
Forest	4.1	MR	46	88	1	Native oakwood	50.8564	-1.6403	30
	4.2	M	69	80	1	Native oakwood	50.8453	-1.5281	20
	4.3	OM	86	68		Native oakwood	50.8327	-1.5173	30
Sitka spruce									
Knapdale	5.5	PT	9	100	2+	Heath/scrub	56.0822	-5.3289	150
	5.1	MR	29	100	2	Heath/scrub	56.0596	-5.5136	160
	5.6	M	44	86	2+	Heath/scrub	56.0635	-5.5087	100
	5.4	OM	82	82	1	Heath/scrub	56.0624	-5.5099	130
Clunes	6.5	PT	10	100	2+	Heath	56.9971	-4.8880	180
	6.1	MR	28	92	2	Heath	57.003	-4.8706	80
	6.2	M	48	95	1	Heath/native woodland	56.9737	-4.9888	330
	6.4	OM	87	100	1	Heath	57.0002	-4.8839	140
Kielder	7.3	PT	16	100	2	Grassland	55.1565	-2.5183	320
	7.1	MR	26	78	2	Grassland	55.1679	-2.4492	260
	7.2	M	43	100	2	Grassland	55.1472	-2.4593	280
	7.4	OM	89	98	1	Grassland/mire	55.1406	-2.4660	310
Glentress	8.6	PT	7	80	2+	Heath/grassland	55.6707	-3.1466	460
	8.1	MR	30	100	2	Heath/grassland	55.6662	-3.1517	380
	8.5	M	49	100	1	Heath/grassland	55.6651	-3.1556	310
	8.4	OM	81	100	1	Grassland	55.6203	-3.1051	290

Appendix 2.2: Environmental variables measured in pre-thicket (PT), mid-rotation (MR), mature (M) and over-mature (OM) pine and spruce study plots.

Location	Study plot number	Stand stage	Age at sampling (years)	Mean basal area (m^2/Ha)	Mean DBH (cm)	Mean stand density (trees/ha)	Mean canopy cover (%)	Mean vegetation cover (%)	Mean litter cover (%)	Mean litter depth (cm)
SCOT'S PINE										
Glen Affric	1.5	PT	4	0.2	3	290	5	118	0	4.6
	1.1	MR	32	4.2	17	173	82	61	43	3.3
	1.2	M	55	6.5	23	150	84	94	7	2.3
	1.3	OM	116	11.6	42	82	69	149	1	2.5
Glenmore	2.6	PT	11	0.6	4	505	26	114	1	2.9
	2.5	MR	28	4.3	20	121	69	117	8	3.6
	2.2	M	52	6.3	23	141	80	101	9	4.2
	2.3	OM	84	8.7	28	136	80	104	12	2.8
Thetford	3.3	PT	8	1.8	5	838	88	39	71	2.7
	3.1	MR	38	6.2	25	124	87	99	77	5.2
	3.5	M	75	5.9	23	133	86	105	45	6.8
	3.6	OM	109	12.0	47	66	80	96	11	5.0
New Forest	4.5	PT	21	2.3	8	545	66	121	7	3.7
	4.1	MR	46	8.7	24	174	88	107	6	3.0
	4.2	M	69	6.5	38	51	72	84	50	3.9
	4.3	OM	86	6.2	20	118	70	110	20	3.5
SITKA SPRUCE										
Knapdale	5.5	PT	9	1.8	7	440	68	101	0	2.8
	5.1	MR	29	4.4	16	203	90	53	44	3.0
	5.6	M	44	13.3	40	99	86	58	38	2.0
	5.4	OM	82	10.3	39	69	85	87	18	2.5
Clunes	6.5	PT	10	0.4	4	320	47	115	0	3.1
	6.1	MR	28	5.1	17	200	89	10	88	2.2
	6.2	M	48	6.5	22	146	88	14	74	2.2
	6.4	OM	87	9.5	40	69	81	66	38	3.2
Kielder	7.3	PT	16	3.4	8	658	73	86	16	4.2
	7.1	MR	26	4.3	16	210	89	73	29	3.4
	7.2	M	43	9.5	28	141	90	50	42	2.6
	7.4	OM	89	5.3	34	51	86	93	3	5.8
Glentress	8.6	PT	7	1.1	5	448	28	103	0	4.4
	8.1	MR	30	5.9	22	141	92	14	85	2.4
	8.5	M	49	10.0	23	201	90	1	98	2.5
	8.4	OM	81	12.7	34	100	75	102	7	3.7

Appendix 2.3: Species lists and average cover (vascular plant and moss) or summed abundance (carabid and spider) of all species identified during 2016 sampling season

Table a) Vascular plant average cover for each forest type split into the four main stages of development. PT represents pre-thicket stand stage, MR represents mid-rotation, M represents mature and OM represents over-mature.

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Acer pseudoplatanus	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Agrostis capillaris	0.00	0.00	1.81	0.22	0.00	0.00	0.00	0.16
Agrostis stolonifera	0.56	0.88	2.03	0.00	1.34	0.00	0.00	1.72
Anthoxanthum odoratum	0.00	0.00	0.31	0.00	0.63	0.00	0.00	0.00
Arrhenatherum elatius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arum maculatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Athyrium filix-femina	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Betula pendula	1.25	0.00	0.00	0.31	0.00	0.00	0.00	0.00
Betula pubescens	0.16	0.03	0.06	0.00	0.00	0.00	0.00	0.00
Blechnum spicant	0.81	0.63	1.53	0.34	1.25	0.03	0.16	0.09
Brachypodium sylvaticum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bromopsis ramosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calluna vulgaris	19.44	3.59	2.34	5.94	32.69	0.00	0.00	0.13
Caltha palustris	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex binervis	0.41	0.00	0.00	0.00	0.13	0.00	0.00	0.09
Carex echinata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex pilulifera	0.00	0.00	0.97	0.00	0.00	0.00	0.00	0.25
Carex remota	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex sylvatica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chamerion angustifolium	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cirsium palustre	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Crataegus monogyna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dactylis glomerata	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
Deschampsia cespitosa	0.66	0.00	0.00	0.00	1.72	0.00	0.56	1.25
Deschampsia flexuosa	6.00	10.66	17.13	8.38	9.50	0.00	0.00	0.19
Digitalis purpurea	0.00	0.00	0.00	0.00	0.16	0.00	0.56	0.09
Dryopteris affinis	0.00	0.00	0.00	0.00	0.94	0.00	0.00	0.66
Dryopteris carthusiana	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.38
Dryopteris dilatata	0.00	0.06	0.25	0.00	0.81	0.34	1.66	7.41
Empetrum nigrum	1.25	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium palustre	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Erica cinerea	0.00	0.00	0.00	0.00	5.41	0.00	0.00	0.00
Erica tetralix	0.63	1.50	0.00	0.31	1.97	0.00	0.00	0.00
Eriophorum vaginatum	0.00	1.41	0.00	0.00	0.00	0.00	0.00	0.00
Euphorbia amygdaloides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fagus sylvatica	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Festuca ovina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fraxinus excelsior	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium aparine	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Galium saxatile	2.13	0.09	1.94	0.13	1.69	0.00	0.00	0.56
Geranium robertianum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glechoma hederacea	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Goodyera repens	0.00	0.00	0.16	0.53	0.00	0.00	0.00	0.00
Hedera helix	0.94	0.00	0.22	0.09	0.00	0.00	0.00	0.00
Holcus lanatus	0.06	0.16	0.00	0.00	0.13	0.00	0.00	0.00
Holcus mollis	1.53	0.00	0.09	0.47	0.00	0.00	0.00	5.03
Hyacinthoides non-scripta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypericum pulchrum	0.25	0.00	0.16	0.06	0.09	0.00	0.00	0.00
Ilex aquifolium	0.00	0.22	0.34	0.06	0.00	0.00	0.00	0.00
Juncus conglomeratus	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Juncus effusus	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63
Juncus inflexus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lonicera periclymenum	2.50	0.41	0.63	0.69	0.00	0.00	0.00	0.00
Luzula multiflora	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Luzula pilosa	0.28	0.00	0.25	0.00	0.00	0.00	0.00	0.50
Lysimachia nemorum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Melampyrum pratense	0.16	0.16	0.00	0.13	0.00	0.00	0.00	0.00
Melica uniflora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mercurialis perennis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Milium effusum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Molinia caerulea	4.28	5.94	9.78	17.19	0.47	0.00	0.00	1.56
Oreopteris limbosperma	0.00	0.00	0.00	0.00	2.22	0.00	0.00	0.31
Oxalis acetosella	0.31	0.00	1.59	0.09	0.22	0.00	4.22	9.78
Phragmites australis	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Picea sitchensis	0.00	0.00	0.00	0.00	0.16	0.00	0.00	1.44
Pinus sylvestris	0.00	0.09	0.06	0.03	0.00	0.00	0.00	0.00
Poa trivialis	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
Polygala vulgaris	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla erecta	0.09	0.97	1.44	0.28	0.56	0.00	0.00	0.00
Primula vulgaris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pteridium aquilinum	11.34	11.41	26.81	31.09	0.00	0.00	0.00	2.34
Quercus robur/petraea	0.09	0.22	0.03	0.00	0.00	0.00	0.00	0.00
Ranunculus ficaria	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus repens	0.94	0.00	0.13	0.00	0.00	0.00	0.00	0.00
Rhododendron ponticum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rosa canina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubus fruticosus	0.25	0.00	1.47	0.28	0.56	0.00	0.03	0.00
Rumex acetosella	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00
Sorbus aucuparia	0.03	0.13	0.19	0.50	0.16	0.00	0.00	0.09
Stellaria alsine	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Stellaria holostea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stellaria media	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Stellaria neglecta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Teucrium scorodonia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trientalis europaea	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Ulex europaeus	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
Urtica dioica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Vaccinium myrtillus	5.00	15.81	0.81	16.56	2.47	0.84	0.00	0.38
Vaccinium vitis-idaea	3.13	5.78	0.06	8.47	0.00	0.00	0.00	0.00
Valeriana officinalis	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica montana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica officinalis	0.28	0.00	0.00	0.06	0.16	0.00	0.00	0.00
Vicia sativa	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Viola riviniana	0.03	0.00	0.56	0.00	0.16	0.00	0.00	0.47

Table b) Moss average cover for each forest type split into the four main stages of development. PT represents pre-thicket stand stage, MR represents mid-rotation, M represents mature and OM represents over-mature.

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Aulacomnium palustre	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Calliergonella cuspidata	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00
Campylopus flexuosus	0.25	0.00	0.09	0.00	0.63	0.00	0.00	0.00
Dicranum majus	0.09	0.16	0.00	0.09	0.72	1.72	0.50	3.00
Dicranum scoparium	0.38	1.22	1.00	0.41	4.00	1.59	0.00	1.00
Eurhynchium striatum	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hylocomium splendens	8.75	7.63	8.28	13.84	0.56	0.00	0.19	0.06
Hypnum cupressiforme	2.19	0.00	0.00	0.00	1.41	0.00	0.00	0.00
Hypnum jutlandicum	2.34	3.75	0.06	0.50	4.19	3.06	1.53	2.19
Kindbergia praelonga	0.94	0.47	4.84	1.56	0.94	6.13	9.03	2.25
Mnium hornum	0.00	0.00	0.00	0.00	0.16	0.28	0.38	7.66
Plagiothecium undulatum	0.19	1.91	1.19	1.22	2.06	7.41	7.34	11.66
Pleurozium schreberi	0.19	2.19	4.78	1.63	1.97	0.00	0.00	0.78
Polytrichastrum formosum	0.00	1.47	0.63	0.25	0.00	0.84	0.00	0.16
Polytrichum commune	2.59	1.50	0.66	0.78	14.03	1.03	0.09	2.75
Pseudoscleropodium purum	0.31	8.44	1.78	1.03	0.00	0.00	0.06	0.16
Ptilium crista-castrensis	0.66	2.22	0.00	1.41	0.00	0.00	0.00	0.00
Rhytidiadelphus loreus	0.13	0.53	0.16	0.31	5.78	4.22	0.09	14.69
Rhytidiadelphus squarrosus	0.25	0.00	1.25	0.00	0.38	0.41	0.00	0.72
Rhytidiadelphus triquetrus	0.00	0.00	0.09	0.16	0.00	0.00	0.00	0.00
Sphagnum capillifolium	0.16	0.00	0.00	0.00	0.78	0.31	0.00	1.41
Sphagnum fallax	0.00	0.00	0.00	0.63	0.00	0.47	0.00	1.25
Sphagnum fimbriatum	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.63
Sphagnum flexuosum	0.00	0.00	0.00	0.00	0.00	0.63	0.00	0.00
Sphagnum girgensohnii	1.09	0.00	0.00	0.00	1.97	0.00	0.00	0.00
Sphagnum palustre	3.13	0.16	0.00	0.09	0.31	0.00	0.00	1.28
Sphagnum quinquefarium	0.16	0.00	0.00	0.00	0.00	3.84	0.00	0.00
Sphagnum rubellum	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphagnum subnitens	0.19	0.41	0.00	2.34	0.56	0.00	0.00	1.19
Thuidium tamariscinum	1.56	0.78	4.09	0.66	3.72	5.09	7.41	3.63

Table c) Carabid summed abundance in each forest type split into the four main stages of development. PT represents pre-thicket stand stage, MR represents mid-rotation, M represents mature and OM represents over-mature.

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Abax parallelepipedus	107	67	445	100	22	1	58	145
Agonum fuliginosum	0	0	0	0	1	0	0	0
Agonum nigrum	0	0	0	0	0	0	0	0
Amara communis	13	0	0	0	0	0	0	0
Amara lunicollis	0	0	1	0	0	0	0	0
Badister bullatus	0	0	0	0	0	0	0	0
Bembidion mannerheimii	2	0	1	0	0	0	0	0
Bradycellus harpalinus	0	0	0	0	1	0	0	0
Bradycellus sharpi	0	0	0	0	0	0	0	0
Calathus micropterus	3	4	18	7	15	30	61	4
Calathus rotundicollis	0	0	2	0	0	0	0	0
Carabus arvensis	0	0	1	0	0	0	0	0
Carabus glabratus	16	5	5	14	20	0	0	8
Carabus granulatus	0	0	0	0	0	0	0	0
Carabus nemoralis	1	4	14	1	0	0	0	0
Carabus problematicus	0	4	20	3	1	1	55	19
Carabus violaceus	3	6	33	7	16	1	8	21
Cychrus caraboides	1	3	8	1	7	1	5	3
Harpalus laevipes	1	0	0	0	0	0	0	0
Harpalus latus	1	0	0	0	2	0	0	0
Leistus rufomarginatus	0	0	0	1	0	0	0	0
Leistus terminatus	1	0	5	6	0	2	11	4
Loricera pilicornis	0	0	0	0	0	0	0	0
Nebria brevicollis	0	0	2	0	0	0	10	4
Nebria rufescens	0	1	0	0	0	0	1	0
Notiophilus biguttatus	0	5	1	0	0	0	1	0
Notiophilus germinyi	1	0	0	1	0	0	0	0
Notiophilus palustris	1	2	0	0	0	0	0	0
Notiophilus rufipes	0	3	3	0	0	0	0	0
Oxypselaphus obscurus	5	0	0	0	0	0	0	0
Platyderus depressus	0	2	0	0	0	0	0	0
Platynus assimilis	0	0	0	0	0	0	5	0
Poecilus cupreus	0	0	0	0	0	0	0	0
Poecilus versicolor	4	0	0	0	0	0	0	0
Pterostichus adstrictus	0	0	0	0	17	0	0	0
Pterostichus aethiops	0	0	0	0	4	0	0	0
Pterostichus diligens	2	0	0	0	2	0	0	0
Pterostichus madidus	95	39	248	77	40	3	79	86
Pterostichus melanaris	0	0	2	0	0	0	0	0
Pterostichus niger	12	25	19	1	30	0	3	18
Pterostichus nigrita	0	0	0	0	0	0	0	1
Pterostichus oblongopunctatus	15	1	38	15	1	0	0	0
Pterostichus rhaeticus	7	0	0	0	0	1	0	0
Pterostichus strenuus	0	1	0	0	13	0	0	0
Stomis pumicatus	0	2	2	1	0	0	0	0
Trechus obtusus	5	0	36	12	115	1	10	16
Trechus rubens	1	0	0	0	2	0	0	0

Table d) Spider summed abundance in each forest type split into the four main stages of development. PT represents pre-thicket stand stage, MR represents mid-rotation, M represents mature and OM represents over-mature.

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Agroeca brunnea	1	0	2	1	0	0	0	0
Agroeca proxima	2	0	0	0	1	0	0	0
Agyneta cauta	0	2	0	0	2	0	0	0
Agyneta conigera	0	0	2	0	0	0	0	0
Agyneta olivacea	1	0	2	0	0	0	0	0
Agyneta ramosa	4	7	2	1	27	3	0	0
Agyneta subtilis	0	2	4	0	0	0	0	0
Allomengea scopigera	0	0	0	0	1	0	0	0
Alopecosa pulverulenta	1	1	0	1	1	0	0	0
Amaurobius fenestralis	0	0	2	0	0	0	0	0
Asthenargus paganus	0	0	0	0	0	3	0	3
Bathyphantes gracilis	0	0	0	1	2	3	0	0
Bathyphantes parvulus	2	0	0	0	0	2	0	0
Centromerus albidus	0	0	0	0	0	0	0	0
Centromerus arcanus	14	35	0	3	55	97	7	27
Centromerus dilutus	3	6	7	9	4	19	6	12
Centromerus incilium	1	0	0	0	0	0	0	0
Centromerus levitarsis	0	0	0	0	0	0	0	0
Centromerus prudens	0	0	0	0	1	0	1	0
Centromerus sylvaticus	1	5	4	3	10	2	0	4
Ceratinella brevipes	0	1	1	1	10	0	0	0
Clubiona reclusa	1	0	0	0	0	0	0	0
Clubiona terrestris	0	1	0	2	0	0	0	0
Cnephalocotes obscurus	0	0	0	0	2	0	0	0
Coelotes atropos	0	0	0	0	2	0	0	0
Coelotes terrestris	0	14	0	0	0	0	0	0
Cryphoeca silvicola	10	3	23	2	0	0	1	2
Dicymbium tibiale	1	0	0	0	2	0	0	0
Diplocephalus latifrons	0	0	0	0	0	0	12	3
Diplostyla concolor	0	6	0	0	0	0	0	0
Dismodicus bifrons	1	0	0	0	0	0	0	0
Drassodes cupreus	1	0	0	0	4	0	0	0
Dysdera erythrina	0	0	0	0	0	0	0	0
Euophrys frontalis	0	0	3	0	0	0	0	0
Gonatium rubellum	0	3	1	4	0	0	0	0
Gongylidiellum vivum	5	0	0	0	0	0	0	1
Hahnia helveola	1	0	0	0	0	0	0	0
Haplodrassus signifer	0	2	0	0	1	0	0	0
Hilaira excisa	1	53	0	1	0	0	0	2
Iberina montana	0	6	8	2	0	0	0	1
Jacksonella falconeri	0	0	1	0	0	0	0	0
Linyphia hortensis	0	0	0	0	0	0	1	0
Macrargus rufus	0	2	6	0	0	0	1	0
Maro minutus	0	1	0	0	0	0	5	1
Metellina mengei	0	0	0	1	0	0	0	1
Metellina merianae	0	0	0	0	0	0	1	1
Micaria pulicaria	3	0	0	0	2	0	0	0
Micaria subopaca	1	0	0	0	0	0	0	0
Micrargus herbigradus	27	32	8	19	51	33	18	27
Microneta viaria	0	1	6	4	0	0	0	0
Minyriolus pusillus	0	0	0	1	1	0	0	0
Monocephalus fuscipes	15	22	13	7	15	36	28	31
Neon reticulatus	2	4	3	1	1	0	0	0
Neriene montana	0	0	0	1	0	0	0	0
Neriene peltata	0	0	0	0	1	0	0	0
Obscuriphantes obscurus	0	0	0	1	0	0	0	0
Oedothorax gibbosus	0	0	1	0	0	0	0	0
Ozyptila trux	0	1	0	1	0	0	0	0
Pachygnatha listeri	0	0	2	1	0	0	0	0
Palliduphantes ericaeus	46	16	8	27	82	34	6	44
Palliduphantes pallidus	2	0	3	8	1	16	5	9
Pardosa lugubris	0	0	1	0	0	0	0	0
Pardosa pullata	26	1	0	0	26	0	0	0

	Scots pine				Sitka spruce			
Species	PT	MR	M	OM	PT	MR	M	OM
Pardosa saltans	5	48	34	52	0	0	0	0
Pelecopsis mengei	0	0	0	0	1	0	0	0
Phrurolithus festivus	2	0	0	0	0	0	0	0
Piratula hygrophila	18	122	314	50	27	0	0	0
Piratula uliginosa	0	0	0	3	7	0	0	1
Pityohyphantes phrygianus	0	0	0	0	0	1	0	0
Pocadicnemis juncea	1	0	0	0	0	0	0	0
Pocadicnemis pumila	2	2	1	1	2	0	0	0
Porrhomma campbelli	0	0	0	1	0	2	1	0
Porrhomma convexum	0	0	0	0	3	1	0	0
Porrhomma montanum	3	5	2	0	1	1	8	4
Porrhomma oblitum	2	0	0	0	0	3	0	0
Porrhomma pallidum	4	16	5	4	10	17	10	10
Robertus lividus	21	13	10	3	33	2	0	7
Saaristoa abnormis	16	32	5	23	39	8	14	12
Saaristoa firma	0	1	0	0	1	1	0	0
Scotina celans	12	0	0	3	0	0	0	0
Scotina palliardii	0	3	0	0	0	0	0	0
Silometopus elegans	0	0	0	0	2	0	0	0
Tapinocyba pallens	9	22	17	13	6	54	8	19
Tapinopa longidens	0	0	0	0	0	1	0	0
Tenuiphantes alacris	5	4	2	17	2	1	3	5
Tenuiphantes cristatus	0	0	0	0	1	0	0	0
Tenuiphantes flavipes	1	25	10	11	0	2	4	0
Tenuiphantes mengei	3	0	0	0	5	0	0	0
Tenuiphantes tenebricola	0	0	3	0	0	7	40	32
Tenuiphantes tenuis	2	0	0	1	0	2	1	0
Tenuiphantes zimmermanni	35	53	89	62	45	136	127	128
Thyreosthenius biovatus	0	1	0	0	0	0	0	0
Tiso vagans	2	0	0	0	0	0	0	0
Trochosa terricola	17	14	6	6	12	0	0	0
Walckenaeria acuminata	9	10	9	6	10	14	4	14
Walckenaeria antica	0	0	0	0	2	0	0	0
Walckenaeria atrotibialis	6	2	2	3	1	0	0	0
Walckenaeria cucullata	9	32	7	16	0	0	0	0
Walckenaeria cuspidata	1	0	0	0	0	0	0	0
Walckenaeria dysderoides	1	0	0	0	0	0	0	0
Walckenaeria furcillata	0	0	0	0	0	0	0	0
Walckenaeria incisa	1	0	0	0	0	0	0	0
Walckenaeria nudipalpis	6	6	4	6	8	14	0	7
Walckenaeria obtusa	0	0	0	0	0	0	0	0
Walckenaeria vigilax	1	0	0	0	1	0	0	0
Xysticus erraticus	0	0	0	0	1	0	0	0
Xysticus luctator	0	0	3	0	0	0	0	0
Zelotes apricorum	0	1	0	0	0	0	0	0
Zelotes petrensis	0	0	0	1	0	0	0	0
Zelotes pusillus	0	0	0	1	0	0	0	0
Zora nemoralis	1	0	0	0	0	0	0	0
Zora spinimana	2	0	1	0	0	0	0	0
Zygiella x-notata	0	1	0	0	0	0	0	6

Appendix 2.4: Mean and standard deviations of species diversity, functional diversity and community weighted mean trait values

Table a: Simpson's index of species diversity means and standard deviation

SD	Vascular plant		Moss		Carabid		Spider	
	mean	SD	mean	SD	mean	SD	mean	SD
Scot's pine	0.63	0.17	0.60	0.13	0.48	0.26	0.80	0.16
Sitka spruce	0.43	0.29	0.70	0.15	0.52	0.29	0.82	0.09

Table b: Rao's quadratic entropy means and standard deviation

FD	Vascular plant		Moss		Carabid		Spider	
	mean	SD	mean	SD	mean	SD	mean	SD
Scot's pine	0.05	0.03	0.22	0.08	0.20	0.12	0.30	0.08
Sitka spruce	0.07	0.07	0.32	0.09	0.19	0.12	0.20	0.07

Table c: Vascular plant trait community weighted mean values and standard deviation

VASCULAR PLANT TRAITS	Height (m)		Seed mass (mg)		SLA (mm^2/mg)	
	mean	SD	mean	SD	mean	SD
Scot's pine	0.68	0.45	0.50	0.50	18.22	3.14
Sitka spruce	0.44	0.14	0.25	0.24	23.58	10.80

Table d: Moss trait community weighted mean values and standard deviation

MOSS TRAITS	Length (cm)		Spore size (µm)		Mat life-form (proportion)		Turf life-form (proportion)		Weft life-form (proportion)	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Scot's pine	140.44	29.96	15.07	1.56	0.16	0.18	0.15	0.15	0.70	0.20
Sitka spruce	140.33	31.42	15.71	2.44	0.28	0.20	0.30	0.22	0.42	0.22

Table e: Carabid trait community weighted mean values and standard deviation

CARABID TRAITS	Size (cm)		Winged (proportion)		Wingless (proportion)		Wing-dimorphic (proportion)		Specialist predator (proportion)		Generalist predator (proportion)		Omnivore (proportion)		Herbivore (proportion)	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Scot's pine	16.80	2.43	0.19	0.23	0.79	0.23	0.02	0.03	0.34	0.38	0.65	0.39	0	0	0.009	0.03
Sitka spruce	14.40	5.44	0.14	0.25	0.83	0.25	0.03	0.05	0.24	0.28	0.76	0.28	0.001	0.002	0.003	0.01

Table f: Spider trait community weighted mean values and standard deviation

SPIDER TRAITS	Size (mm)		Ballooning (proportion)		Running hunter (proportion)		Sheet web-weaver (proportion)		Space web-weaver (proportion)		Orb web-weaver (proportion)		Ambush hunter (proportion)	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Scot's pine	3.71	1.04	0.63	0.17	0.33	0.32	0.59	0.31	0.03	0.04	0.002	0.004	0.008	0.01
Sitka spruce	2.61	0.37	0.64	0.15	0.04	0.09	0.93	0.10	0.02	0.03	0.006	0.01	0.001	0.002

Appendix 2.5: Summary statistics of GAMM

Table a: Summary statistics from Simpson's diversity index general additive mixed models

Tree species	Taxon	Adj R^2	Age			Random term (location)
			p value	F statistic	edf	p value
Scot's pine	vascular	0.560	0.944	0.005	1	0.004
	moss	0.244	0.654	0.211	1	0.081
	carabid	0.592	0.714	0.142	1	0.003
	spider	0.503	0.062	3.275	2.897	0.111
Sitka spruce	vascular	0.410	0.045	5.098	1	0.104
	moss	0.022	0.547	0.809	1.502	NA
	carabid	0.544	0.100	2.623	3.086	0.138
	spider	0.394	0.174	1.993	2.07	0.082

Table b: Summary statistics from Rao's quadratic entropy general additive mixed models

Tree species	Taxon	Adj R^2	Age			Random term (location)
			p value	F statistic	edf	p value
Scot's pine	vascular	0.253	0.824	0.051	1	0.072
	moss	0.542	0.097	2.537	2.113	0.033
	carabid	0.540	0.658	0.206	1	0.006
	spider	0.332	0.195	1.758	2.124	0.094
Sitka spruce	vascular	0.006	0.454	0.501	1.175	NA
	moss	0.333	0.064	2.986	2.147	NA
	carabid	0.536	0.031	3.950	3.603	NA
	spider	0.664	0.001	9.426	2.698	NA

Table c: Summary statistics from CWM GAMM

Tree species	Taxon	Trait	Adj R^2	Age			Random term (location)
				p value	F statistic	edf	p value
Scot's pine	Vascular	height	0.623	0.461	0.583	1	0.002
		seed	0.552	0.946	0.005	1	0.004
		SLA	0.516	0.179	2.048	1	0.014
	Moss	size	0.575	0.817	0.056	1	0.003
		spore	0.092	0.380	1.012	1.875	NA
		mat	0.187	0.082	3.530	1	0.290
		turf	0.579	0.232	1.978	1.991	0.008
		weft	0.346	0.033	4.154	1.595	NA
	Carabid	size	0.318	0.750	0.106	1	0.044
		wingless	0.322	0.647	0.541	1.275	0.057
		winged	0.287	0.487	0.515	1	0.073
		specialist	0.917	0.430	0.905	1.129	1.15E-11
		generalist	0.889	0.711	0.418	1.495	5.69E-09
	Spider	size	0.789	0.853	0.036	1	1.86E-05
		ballooning	0.026	0.738	0.116	1	0.285
		running	0.704	0.970	0.001	1	0.0003
		sheet	0.648	0.784	0.079	1	0.001
		space	0.531	0.070	3.497	2.22	0.070
Sitka spruce	Vascular	height	0.243	0.115	2.542	1.776	NA
		seed	0.125	0.309	1.394	1.865	NA
		SLA	0.113	0.373	1.324	1.887	NA
	Moss	size	0.557	0.007	6.297	2.599	NA
		spore	0.241	0.031	5.753	1	NA
		mat	0.383	0.221	1.675	1.973	0.071
		turf	0.469	0.020	4.743	2.477	NA
		weft	0.100	0.719	0.195	1.39	0.224
	Carabid	size	0.344	0.043	4.019	1.692	NA
		wingless	-0.033	0.468	0.560	1	NA
		winged	-0.043	0.529	0.419	1	NA
		specialist	0.380	0.373	0.863	1	0.037
		generalist	0.407	0.392	0.795	1	0.029
	Spider	size	0.595	0.006	6.267	3.088	NA
		ballooning	0.100	0.124	2.668	1	NA
		sheet	0.691	0.001	9.506	3.027	NA
		space	0.399	0.040	4.149	2.346	NA

Chapter 3

Re-visiting forest stands 20 years on: is there evidence of taxonomic and functional homogenisation in vascular plant, bryophyte and beetle assemblages?

Introduction

Anthropogenic pressures, such as over-exploitation of resources, habitat change, nutrient loading, invasive species introductions and climate change, are key contributors to biodiversity declines globally (Ceballos et al., 2015; Dirzo et al., 2014; Diversity, 2006). A form of biodiversity loss gaining attention is biotic homogenisation. This refers to increasing taxonomic, functional or genetic similarity of communities, or put simply, reduced ß diversity (McKinney and Lockwood, 1999; Olden et al., 2004). Biotic homogenisation was initially recognised to be occurring as a consequence of the introduction of invasive species (McKinney and Lockwood, 1999). Biotic homogenisation has since been associated with an intensification of land-use leading to habitat changes (Olden et al., 2004). Taxonomic and functional homogenisation can occur where there is: 1) a significant increase in the frequency or abundance of common species, non-native species and/or of species with comparable traits (e.g. effective dispersal ability), 2) a decline in the frequency or abundance of rare species, endemic species and/or of species with unique traits, 3) combinations of the two (Olden et al., 2004).

A consequence of biotic homogenisation is a reduced range of responses by communities to environmental change and a reduced pool of species capable of compensating for extinctions which affects resistance and resilience to perturbations at the landscape scale (Olden et al., 2004). Functional and taxonomic homogenisation are intrinsically linked since the likelihood of a species increasing or decreasing in abundance or frequency depends on its functional traits or life-history attributes and their interaction with the environment (Olden and Rooney, 2006).This means biotic homogenisation could threaten ecosystem function and the provision of ecosystem services making it an important process to monitor (Clavel et al., 2011; Olden et al., 2018, 2004).

There is a growing body of evidence that biotic homogenisation is occurring across taxonomic groups and biomes (Baiser et al., 2012; Olden et al., 2016). This is despite a

research bias on this topic towards fish and vascular plant studies and little consideration of functional homogenisation altogether. In forests specifically, there is evidence for both taxonomic and functional homogenisation of understorey vegetation communities (Baeten et al., 2012; Hester et al., 2019; Keith et al., 2009; Rooney et al., 2004; Smart et al., 2006). This would appear to be the result of generalist species increasing in cover or frequency over time and the loss of specialists (Rooney et al., 2004). This is a common observation in studies of biotic homogenisation since the loss of localised species and/or spread of more common species is thought to drive homogenisation of communities (Clavel et al., 2011). Specialist species, by definition, should be more vulnerable to habitat changes since they have narrower niches, whereas generalists can tolerate a broader range of conditions (Büchi and Vuilleumier, 2014; Clavel et al., 2011; Lawton, 1994; van Schalkwyk et al., 2019). In addition, generalists may benefit from reduced competition in the absence of specialists (Büchi and Vuilleumier, 2014). Other characteristics expected to cause species to be vulnerable to declines include low fecundity, slow growth and poor or slow dispersal (Büchi and Vuilleumier, 2014; Lawton, 1994; McKinney and Lockwood, 1999).

The study of biotic homogenisation in arthropod communities is particularly limited. This is of concern when considering recent evidence of significant declines in the biomass, abundance and species richness of insects over recent decades (Brooks et al., 2012; Hallmann et al., 2017; Seibold et al., 2019). This information can additionally provide information on the drivers of change, which are essential to preventing or reversing such declines. For example, Gámez-Virués et al. (2015) have shown, by investigating changes in arthropod functional traits, that changes in arthropod communities are driven by landscape simplification and intensive management at the local scale in agricultural fields.

Biotic homogenisation and general declines in diversity have been detected in forest vegetation communities, although this has often been less severe in comparison to a variety of open habitats (Baeten et al., 2012; Brooks et al., 2012; Hester et al., 2019; Keith et al., 2009; Rooney et al., 2004; Seibold et al., 2019). However, many of these studies have

focussed on vascular plants only or mainly sampled in unmanaged or semi-natural forests. Given that biotic homogenisation is expected to result from habitat change due to intensification of human land-use, this form of diversity loss could be expected to occur in some of the most intensively managed forests and it is suggested that this is where our efforts should be focused (Olden et al., 2016). Commercial plantation forests are among the most intensively managed forest types and, therefore, the communities within may be more vulnerable to biotic homogenisation (Sing et al., 2017). It is especially important to establish whether biotic homogenisation is occurring in those regions where forest cover is low and/or where a high proportion of forest cover is intensively managed since these forests can play an important role in the delivery of many forest-related ecosystem functions and services (Bauhus et al., 2009; O'Callaghan et al., 2017).

It has been suggested that the most reliable way to study changes in community composition is to sample the same sites at different points in time rather than use space for time substitution (Olden, 2006; Rooney et al., 2004). In addition, since biotic homogenisation occurs at the regional-scale, study sites should cover a wider geographical range (Rooney et al., 2004). This type of study design is laborious and therefore rare and usually restricted to single taxonomic groups, particularly vascular plants for which long-term monitoring data more commonly exists (eg. Rooney *et al.*, 2004; Smart *et al.*, 2006). This is despite the suggestion that multi-taxa studies of biotic homogenisation could greatly improve our understanding (Olden et al., 2016). Combining taxonomic and functional homogenisation could further enhance our understanding of patterns since functional traits are able to reveal the mechanisms behind changes in species composition (Clavel et al., 2011; Olden et al., 2018).

This study will determine whether biotic homogenisation of communities is occurring in three forest types (oak, Sitka spruce, Scots pine) over a 20-year period. We predict that there will be declines in species richness, taxonomic and functional diversity and beta diversity, with corresponding changes in community composition. The functional response traits of species

increasing and decreasing in abundance/cover and/or frequency are predicted to be different. Specifically, species lost or less common over time will have trait values representing poor dispersal ability and specialist resource use/acquisition abilities, whereas more common and new species will have trait values represent good dispersal and wider niches.

Methods

Study locations

The study took place at 12 forest locations across in Great Britain, using three common forest types. At each location, forest stands were selected which were dominated by Sitka spruce (*Picea sitchensis* Bong. Carrière), Scots pine (*Pinus sylvestris* L.) or oak (*Quercus robur-petraea* L. – oak*)* (Figure 3.1). Together these three forest types make up around 41% of Great Britain's forest cover (Forest Research, 2019). The forests selected for study are managed by the common silvicultural system of clear-cutting and replanting with the exception of the oak stands. While the traditional definition of a semi-natural forest suggests that a forest must not be obviously planted, Peterken (2019) recommends that we relax our definition of natural woodlands to include forests that have been allowed to develop naturally after an intervention. Indeed, the European Forest Institute already includes this type of forest in their definition of semi-natural forest (Schuck et al., 2002). The oak forests in this study are of planted origin however, they were planted on ancient woodland sites, with native tree species and are predominantly managed for conservation purposes. Several of the sites have statutory designations as a result of the quality of oak forest habitat they provide.

To ensure that our assessments represented the biodiversity associated with the successional stages across the plantation cycle, stands were selected from the key stages of forest development appropriate to that forest type. For the conifer species this formed a chronosequence of four stages representing: young forest prior to canopy closure (4-21 years old in Scots pine and 7-16 years in Sitka spruce), closed canopy forest (28-46 years old in Scots pine, 26-30 in Sitka spruce and 60-128 in oak), commercially mature forest (52-75 years old in Scots pine, 43-49 in Sitka spruce and 108-197 in oak) and long-term retention forest that has not been felled at commercial maturity for the purposes of conservation of biodiversity (84-116 years old in Scots pine and 81-89 in Sitka spruce).

Stand ages in each of these categories differed between tree species to ensure chronosequences encompassed similar developmental stages for all tree species. One Scots pine chronosequence (Thetford) did not include an over-mature stand due to a lack of availability. Also, for oak, only two of the four stages of development were available since young oak and very old oak stands are not common in Great Britain and those that are available are not of sufficient size or within suitable locations for a replicable study (Humphrey et al., 2003). In total we selected 39 stands in four chronosequences of both Sitka spruce and Scots pine and four partial sequences of oak (Figure 3.1). All stands were at least 2.5ha and within large forested areas to reduce the influence of non-forested habitat. Within a chronosequence, stands were matched for similar soils, topography, site history, climate, location and elevation where possible (see Appendix 3.1 for details of stand characteristics). Distances between stands within a chronosequence ranged from 0.15-16 km (median 4.2 km) and distances between chronosequences were 10-750 km (65-750 km for Scots pine (median 650 km), 65-350 km for Sitka spruce (median 170km) and 60-725 km for Oak (median 635 km)).

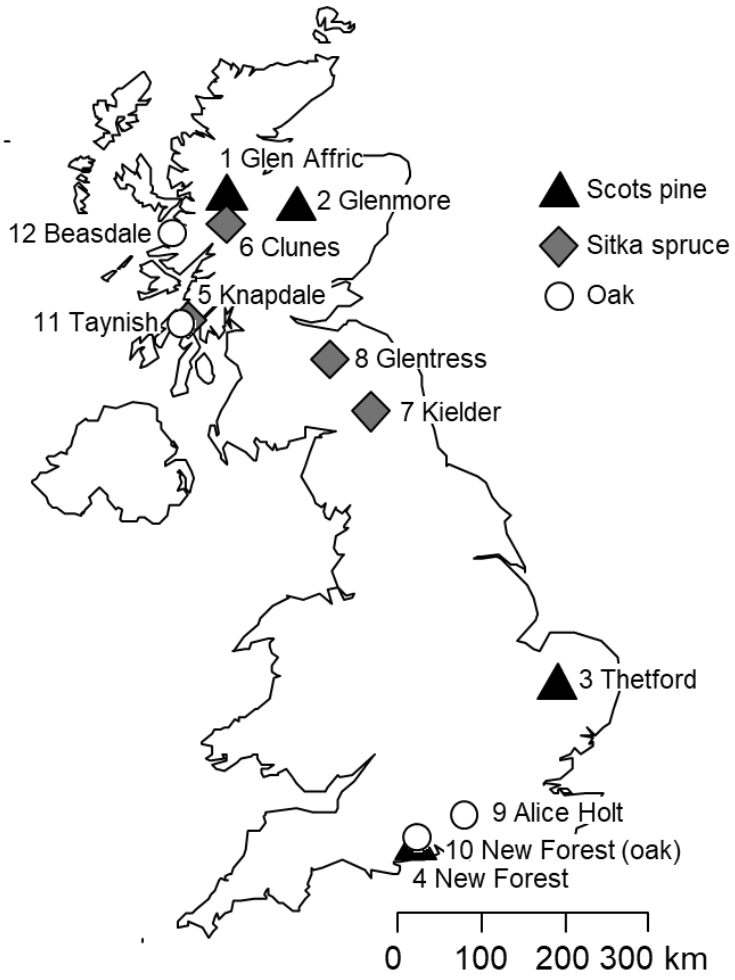


Figure 3.1: Locations of four Sitka spruce, four Scots pine and four Oak clusters across Great Britain. Each cluster of Sitka spruce and Scots pine is comprised of four stands, each representing four different stages of forest development and each oak cluster is comprised of two stands, each representing two different stages of forest development. Black triangles indicate the locations of Scots pine, grey diamonds the locations of Sitka spruce and white circles the location of oak. The same symbols are used for each forest type in all relevant figures throughout this chapter.

Data collection

Three taxonomic groups (vascular plants, mosses and carabid beetles) were surveyed in a one ha square study plot positioned centrally within each stand and at least 30m from the edge of the stand. The three taxonomic groups were originally surveyed between 1995 to 1998 (Humphrey et al., 2003) (Sample Period 1) and resurveyed using the same protocols in 2016 and 2017 (Sample Period 2). Where the exact stand was no longer available in sampling Period 2 for resurvey (e.g. due to replanting with an alternative forest type), a matched alternative at the same developmental stage within the same forest was selected. Matched alternative stands were required in 10 cases and these are indicated in Appendix 3.1

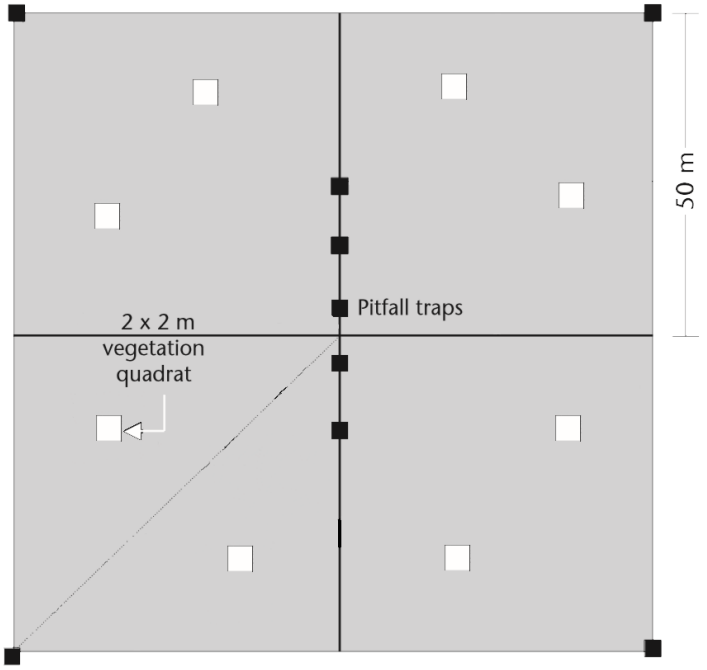


Figure 3.2: Study plot design amended from Humphrey, Ferris and Quine, 2003

Vascular plant and moss assessment

Each one ha study plot was split into four 50x50m quarters and each quarter was then split again in half diagonally. Vegetation quadrats measuring 2x2m were placed within each half, resulting in eight quadrats per study plot (Figure 3.2). Percentage cover to the nearest five percent was estimated for all species of vascular plant and moss in both sampling periods. Plot averages for each species were calculated based on these eight quadrats. Atherton et al. (2010) and Rose (2006, 1989) were used to identify mosses and vascular plants, respectively.

Carabid sampling

Pitfall traps were used to collect ground-active carabid beetles. Catches are biased towards more active, epigeal invertebrate species, and so represent relative activity-density of this group rather than absolute abundance of whole ground-dwelling communities (Thiele, 1977). Five pitfall traps were installed in a line running north to south through the centre of

each study plot, with traps spaced at 10m intervals (Figure 3.2). Traps were 75mm in diameter, 110mm deep and contained 50ml of undiluted propylene glycol (antifreeze) as a temporary preservative. A 20x20cm galvanised steel cover was positioned approximately three cm above the ground over the traps to prevent flooding of the traps, debris falling in and to minimise access by small mammals. These lids each had 15cm-wide entrance holes at all four corners which were kept clear of leaf litter and any other debris. In areas with high densities of potentially disruptive mammals (New Forest and all Oak stands), traps were protected from trampling at these locations by a 250x250mm gauge mesh cage held in place by metal pegs. Neither lids nor mesh cages have been found to affect pitfall trapping efficiency (Siewers et al., 2014). The traps were run from the beginning of May for 20 consecutive weeks at each study plot for two consecutive years in Sampling Periods 1 and 2. During Sampling Period 1 all traps were not run for the same two consecutive years between 1995 and 1998 (Table 3.1). During Sampling Period 2, traps were run at all locations in 2016 and 2017. Traps were reset every two weeks during Sampling Period 1 but, due to logistical constraints, this was changed to every four weeks during Sample Period 2. Samples were pooled across the 20 weeks and two years for each sampling period. All carabid beetle species were identified using Luff (2007).

Table 3.1: Sampling periods for all locations during both sampling periods

Location	Pitfall traps active Sampling period 1	Pitfall traps active Sampling period 2	Years between sampling periods
1 Glen Affric	1996-97	2016-2017	20
2 Glenmore	1996-97	2016-2017	20
3 Thetford	1995-96	2016-2017	21
4 New Forest (pine)	1995-96	2016-2017	21
5 Clunes	1995-96	2016-2017	21
6 Knapdale	1995-96	2016-2017	21
7 Kielder	1996-97	2016-2017	20
8 Glentress	1996-97	2016-2017	20
9 Alice Holt	1997-98	2016-2017	19
10 New Forest (oak)	1997-98	2016-2017	19
11 Taynish	1997-98	2016-2017	19
12 Beasdale	1997-98	2016-2017	19

Functional trait selection

For each taxonomic group, two functional response traits were selected that were considered to reflect vulnerability to local extinction via a variety of pressures thought to be

present in the Anthropocene (e.g. habitat fragmentation, loss and modification) and ability to track or tolerate environmental change. The first was dispersal ability which was represented by adult wing-form in carabids, seed mass in vascular plants and spore size in mosses. Poor dispersers (e.g. large seeds/spores and wingless carabids) are comparatively limited in their ability to move when subject to changing conditions or survive in fragmented landscapes (Lawton, 1994; Lönnell et al., 2014; Niemelä, 2001). The second was related to resource acquisition where the resource is thought to be a main limiting resource for the taxonomic groups considered (i.e. light for vascular plants, water for mosses and type of prey for carabids) (Decocq et al., 2004; Guillemain et al., 1997; Proctor et al., 2007). Species that have more specialist resource requirements (e.g. plants with low SLA, mosses with mat life-forms and carabids with a specialist diet) are more likely to be affected by changing conditions and less likely to find suitable habitat or specific resources elsewhere (Thuiller et al., 2005; Tiselius et al., 2019).

Trait values for each species were derived from published databases and literature (Appendix 3.2). Sources were as follows: vascular plants - LEDA (Kleyer et al., 2008), mosses – BRYOATT (Hill et al., 2007), carabids - Carabids.org (Homburg et al., 2014) and Luff, (2007).

Data analysis

Data preparation

For carabids, to account for any differences in trapping effort between study plots, the abundance of each species in each plot was divided by the number of trap days in that plot and multiplied by the maximum number of trap days in all plots. Trap days per year varied from 135-141, except at one site where, due to logistical reasons, traps were open for only 85 days during one of the sampling seasons. This information was not available for Sampling Period 1 data and number of trap days was assumed to be equal.

Changes in species richness, species diversity and functional diversity between Sampling Periods 1 and 2

Species richness (SR) was determined after removing rare species. A species was considered rare if it occurred once across all sampling periods (abundance of one for carabids and in one quadrat with less than 1% cover for vascular plants or mosses).

Species removed due to infrequent occurrences included 10 vascular plant species in pine (0.2% of total cover), 6 in spruce (0.2% of total cover) and 18 in oak stands (1% of total cover). For mosses we excluded from the dataset, three rare species in spruce (0.1% of total cover) and one in oak stands (0.2% of total cover). In addition, we excluded two rare carabid species in pine (0.03% of individuals), one in spruce (0.02% of individuals) and four in oak stands (0.04% of individuals). We decided against using a more conservative limit in order to strike a balance between including rare species which may have been missed in any given year and discounting rare species which were expected to be lost over time. Sample-based rarefaction was used to estimate SR. This method corrects for differences in sampling effort which can highly influence the number of species observed in samples (Chao and Chiu, 2016).

Simpson's index of species diversity was used as a measure of species diversity (SD) (Simpson, 1949) and Rao's quadratic entropy index was used as a measure of functional diversity (FD) (Botta-Dukát, 2005; Rao, 1982). SD is weighted by relative-abundance and FD is a commonly used measure of the abundance-weighted variance of dissimilarities between species pairs that was adapted from SD for use with functional trait data (Botta-Dukát, 2005). FD was calculated from a distance-matrix of all traits for each taxon using Gower dissimilarity since a combination of numerical and categorical traits were chosen. Abundance-weighted measures were used to compliment SR since the way each metric considers abundance or cover has different consequences for the influence of dominant and rare species on results (de Bello et al., 2007). FD cannot be calculated for communities

with fewer species than there are traits. This occurred with carabid communities in two spruce plots during sampling period two. FD was assumed to be 0 for these plots.

To determine if diversity was lost between sampling periods 1 and 2, Paired T tests were used to test for differences in SR, SD and FD. Where one of a pair of plots had zero total abundance, both plots from the pair were removed from datasets of both sampling periods.

Compositional shifts over sampling periods

Where there was zero total abundance of a taxonomic group in a study plot during a sampling period, these samples were excluded from the dataset since analysis could not be carried out for these study plots. This included vascular plants in one mature spruce study plot in sampling period one sampling and one mid-rotation spruce plot in sampling period two. Both plots were in Kielder.

As a measure of changes in community composition due to turnover of species, changes in species-based community composition (abundance x plot matrices) were tested using permutational multivariate analysis of variance (PERMANOVA) with Euclidean distances. Abundance matrices were Hellinger transformed to ensure that results accounted for changes in rarer species as well as the most abundant. Permutations were constrained within chronosequences to account for variation due to geographic location.

Community Weighted Means (CWM) of each trait were calculated as a measure of functional composition using the traits listed in Appendix 3.2. For continuous traits, CWMs estimate the average trait value in a community, weighted by the relative abundance of each species. For categorical traits, this calculates the proportion of individuals with each trait value per community. Species with missing trait information were removed only if they occurred infrequently since CWMs cannot be calculated for species with missing trait data. This is considered acceptable if the commonest species and at least 80% of species and cover/abundance are included (Pakeman, 2014). A total of eight species of vascular plant and one species of carabid had missing trait data. These accounted for 0.5-1% of the total

cover of vascular plants in each forest type and 2 carabid individuals in pine forests accounting for 0.06% of all carabids in this forest type. Most species with missing data occurred in one or two plots, but none occurred in more than 9 plots. CWM x plot matrices were standardised to zero mean and unit variance before undergoing PERMANOVAs.

Changes in dispersion over sampling periods

Dispersion, defined here as the variability in species composition or CWMs within a forest type, was measured using multivariate homogeneity of group variance with Euclidean distances carried out on Hellinger transformed abundance x plot matrices and standardised CWM x plot matrices (Anderson et al., 2006). This measures the average dissimilarity of individual samples to the group centroid. In order to assess if nestedness patterns were present, differences in dispersion between sampling periods were tested using pairwise permutation tests. To visualise shifts in community composition and dispersion over time, unconstrained redundancy analysis (RDA) conditional on chronosequence location were created.

Winners and losers

To identify which species are driving observed changes in diversity and composition, relative species dominance values (DV), proposed by Pinzón and Spence (2010), were calculated for all species in each sampling period. DV is the product of the relative abundance and relative frequency of species and can be used to distinguish between five dominance categories: dominant (the most abundant and frequently encountered), sub-dominant (frequent but with lower abundances), locally-dominant (high abundance but at fewer sites), common (lower abundance and frequency) and uncommon species (lowest abundance and frequency). A species was considered a “winner” if it increased in dominance (higher dominance category in Sampling Period 2) and a “loser” if dominance declined between sampling periods (lower dominance category in Sampling period 2). If the dominance value of a species changed by more than 20% (with a DV of 100% indicating it is the only species in a community), it was considered to have undergone a notable change.

This can occur without a species changing dominance categories. To determine if species were being selected according to their functional response traits, the trait values of 'winners' and 'losers' species were compared using Fligner-Killeen tests (continuous traits) and Fisher's exact tests (categorical traits).

All analyses were carried out in R (R Core Team, 2019). The following packages and functions were used in the analysis: Base R package (R Core Team, 2019), package "iNEXT" for estimating SR (Chao *et al.*, 2014; Hsieh *et al* 2019), function "melodic" for calculating SD and FD (de Bello et al., 2016), function "trova" to calculate the distance matrix used by function "melodic" (De Bello et al., 2013), package "stats" for paired T tests, Fligner-Killeen tests and Fisher's exact tests (R Core Team, 2019), package "FD" for CWMs (Laliberté and Legendre, 2010; Laliberté *et al* 2014) and package "vegan" for data transformation and standardisation, PERMANOVAs, beta dispersion and permutational testing of beta dispersion (Oksanen et al., 2019). "vegan" and "ggplot2" packages were used to produce ordination plots and bar plots, respectively (Oksanen et al., 2019; Wickham, 2016). All analyses used relative abundance data so that absolute changes in abundance did not influence results.

Results

Overview

During the first sampling period, 142 species of vascular plants were identified (61 species in pine, 56 in spruce and 100 in oak forests) whereas only 94 species were identified in the second sampling period (56 species in pine, 38 in spruce and 64 in oak forests). 36 species of moss were identified from the forest floor during sampling period one (24 species in pine, 27 in spruce and 27 in oak forests) and 32 were identified in the second sampling period (26 species in pine, 24 in spruce and 19 in oak forests). During sampling period one a total of 13,228 individuals of 42 species of carabid were identified (3177 individuals of 28 species in pine, 2130 of 27 species in spruce and 7921 of 25 species in oak forests), whereas 6763 individuals of 49 species were sampled in sampling period two (2292 individuals of 39 species in pine, 1629 of 32 species in spruce and 2842 of 29 species in oak forests). See Appendix 3.3 for cover/abundance of species recorded across stand types.

Changes in species richness, species diversity and functional diversity over time

Significant declines in SR between P1 and P2 were observed only among vascular plants in oak plantations and mosses in spruce and oak plantations Carabid SR did not change over the time period in any forest type and no changes in SR were detected for any taxon in pine forests (Figure 3.3; Table 3.2). Across all taxa and forest types there was a trend for declining SD over time, except that of vascular plants in pine forests, which increased significantly. Declining SD trends were significant only for vascular plants in spruce forests and for mosses in pine and oak forests (Figure 3.4). Again, no changes in SD of carabid communities were detected. In contrast, FD showed varied responses over time and among the forest types. Vascular plant FD decreased significantly over time in spruce forests whereas moss FD was significantly lower in oak. Finally, carabid FD did not change significantly between sampling periods in pine or spruce forests but there was a weak

decline in oak forests (Figure 3.4). See Table 3.2 for a summary of test outputs for SR, SD and FD.

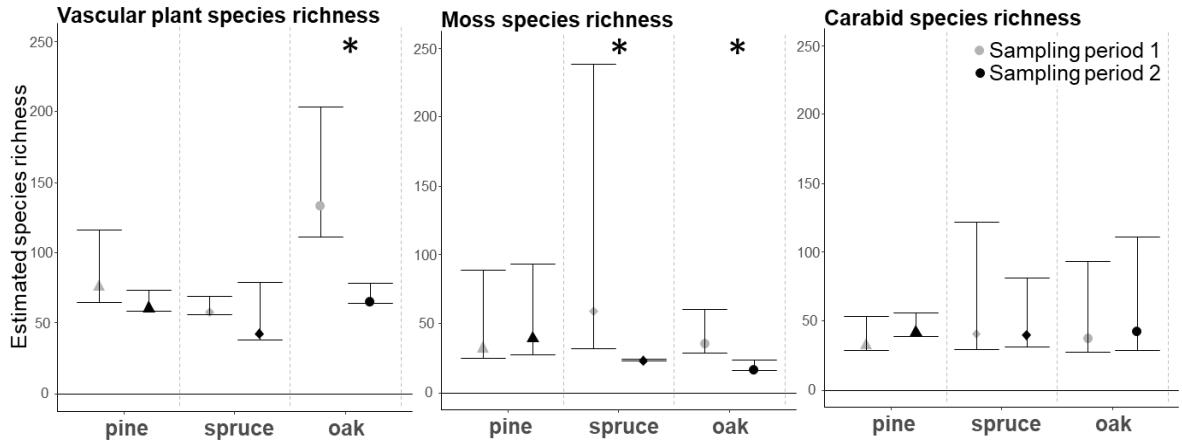


Figure 3.3: Estimated species richness of each sampling period based on rarefaction showing mean richness and upper and lower confidence limits (95%). Where confidence intervals do not overlap, a significant difference between sampling periods is indicated by an asterisk.

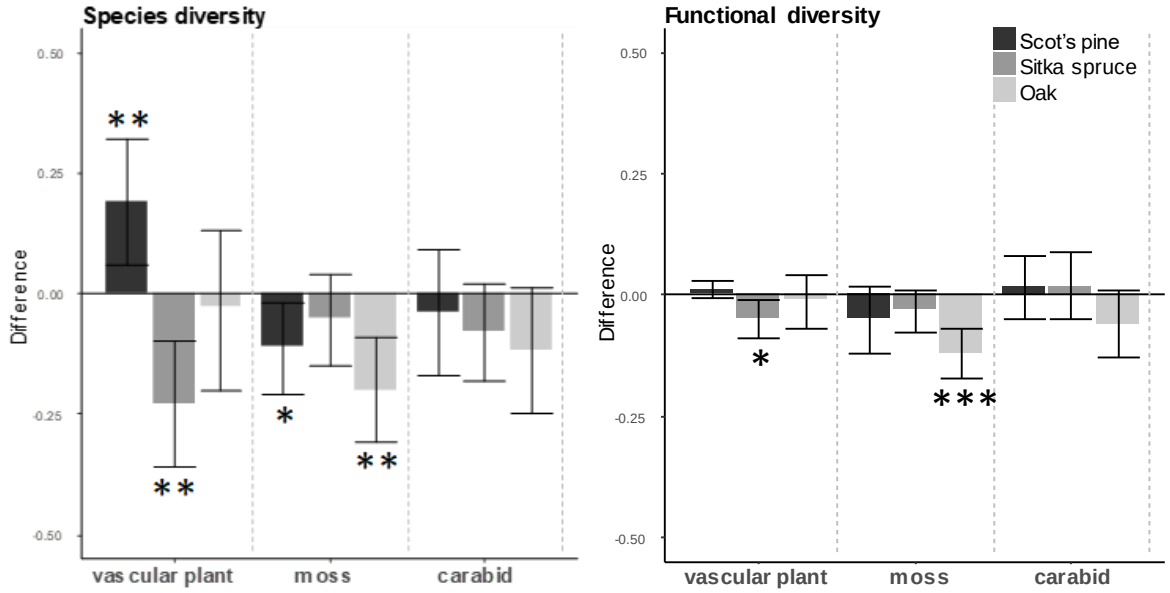


Figure 3.4: The average change in species diversity (SD) and functional diversity (FD) of vascular plants, mosses and carabids between sampling period 1 and 2. Bar charts indicate 95% confidence intervals and are grouped by taxa and tree species. Negative bars indicate a decline since sample period 1. Significant paired T tests are indicated by asterisks (p<0.05; ** p<0.01; *** p<0.001).*

Changes in composition and dispersion between Sampling Period 1 and Sampling Period 2

For nearly all taxonomic groups, species-based and functional trait-based community composition did not change over time in the different stand types. Similarly, there was no difference in beta dispersion of communities for any taxonomic groups in any of the forest types over time (Table 3.2, Figures 3.5-6). Exceptions to these findings include a significant shift in the taxonomic composition of carabids in oak stands and a weak significant difference of this taxonomic group in Scots pine and Sitka spruce over time. The composition of mosses in pine stands and vascular plants in oak also demonstrated a near significant change in species composition between over time. The only differences in functional composition that were detected were among moss and carabid communities in oak forests which had near-significant shifts in functional trait composition, along with moss communities in pine forests

Table 3.2: Changes between Sampling Period 1 and Sampling Period 2 in the SR, SD, FD, composition and beta dispersion for vascular plant, moss and carabid communities in Scots pine, Sitka spruce and oak stands. For species richness results, significant changes are indicated by S and non-significant changes by NS. Dark grey shading highlights significant changes (p<0.05) and light grey shading highlights weak trends.

	VASCULAR PLANTS		**MOSS**		**CARABIDS**	
	difference	p value	difference	p value	difference	p value
SCOT'S PINE						
SR		NS		NS		NS
SD	0.19	**0.01**	-0.11	**0.03**	-0.04	0.49
FD	0.01	0.15	-0.05	0.13	0.02	0.54
taxonomic composition		0.36		0.06		0.07
functional composition		0.45		0.08		0.17
taxonomic beta dispersion		0.21		0.74		0.70
functional beta dispersion		0.28		0.17		0.67
SITKA SPRUCE						
SR		NS	-	**S**		NS
SD	-0.23	**0.001**	-0.05	0.26	-0.08	0.13
FD	-0.05	**0.02**	-0.03	0.15	0.02	0.51
taxonomic composition		0.24		0.13		0.06
functional composition		0.72		0.11		0.45
taxonomic beta dispersion		0.49		1		0.35
functional beta dispersion		0.65		0.74		0.32
OAK						
SR	-	**S**	-	**S**		NS
SD	-0.03	0.66	-0.2	**0.004**	-0.12	0.06
FD	-0.01	0.58	-0.12	**0.0005**	-0.06	0.10
taxonomic composition		0.10		0.11		**0.003**
functional composition		0.93		0.06		0.10
taxonomic beta dispersion		0.61		0.91		0.43
functional beta dispersion		0.68		0.35		0.45

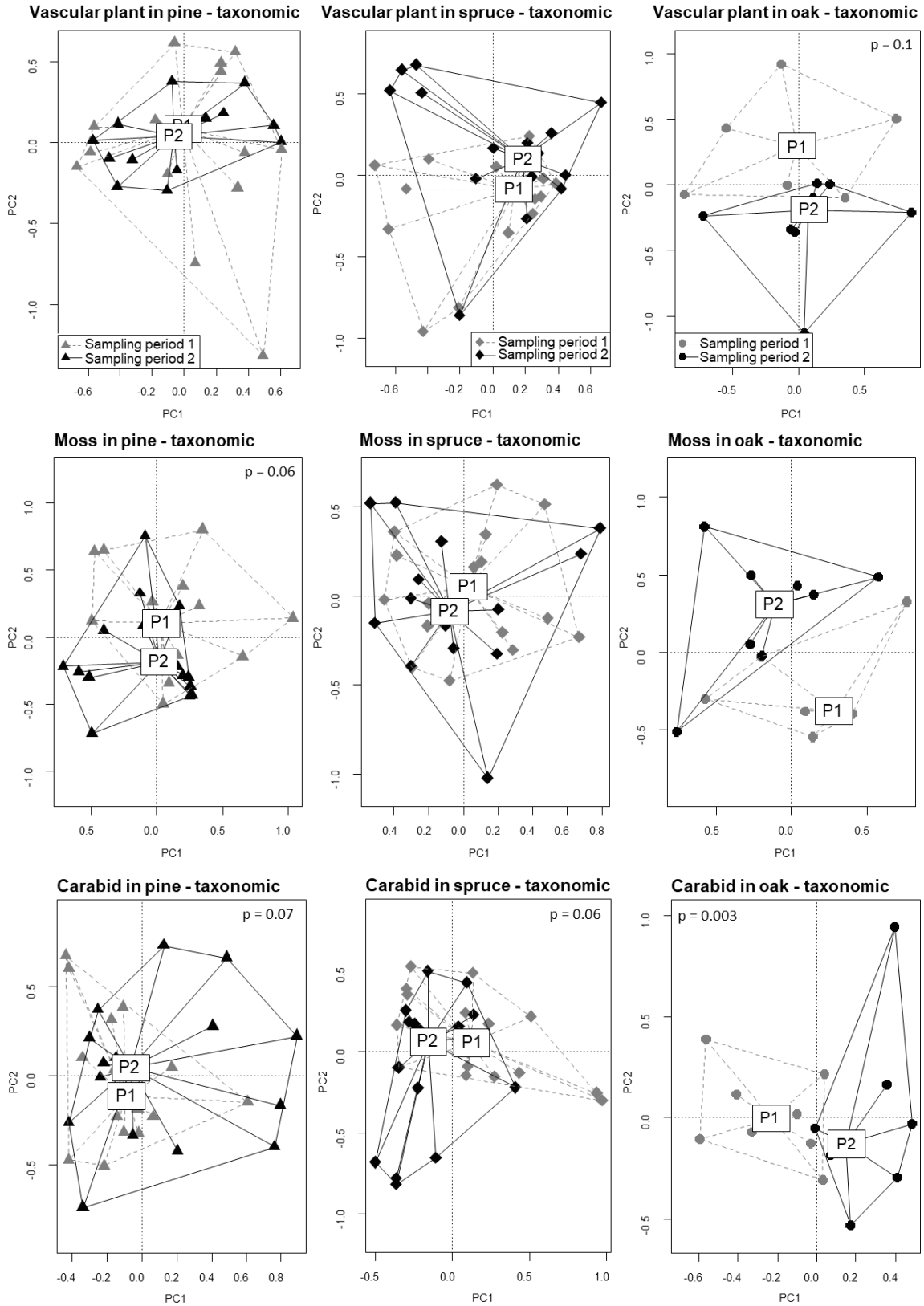


Figure 3.5: Taxonomic-based unconstrained RDA ordinations of vascular plant, moss and carabid communities in Scots pine plantations, Sitka spruce plantations and semi-natural oak forests showing samples grouped by sampling period. Variation due to chronosequence location is partialled out. Sample period 1 (P1) is indicated by grey points and dashed lines and sample period 2 (P2) is indicated by black points and solid lines. P1 and P2 boxes indicate centroids of communities for the respective sampling period. Significant and near-significant p values are indicated on plots where applicable.

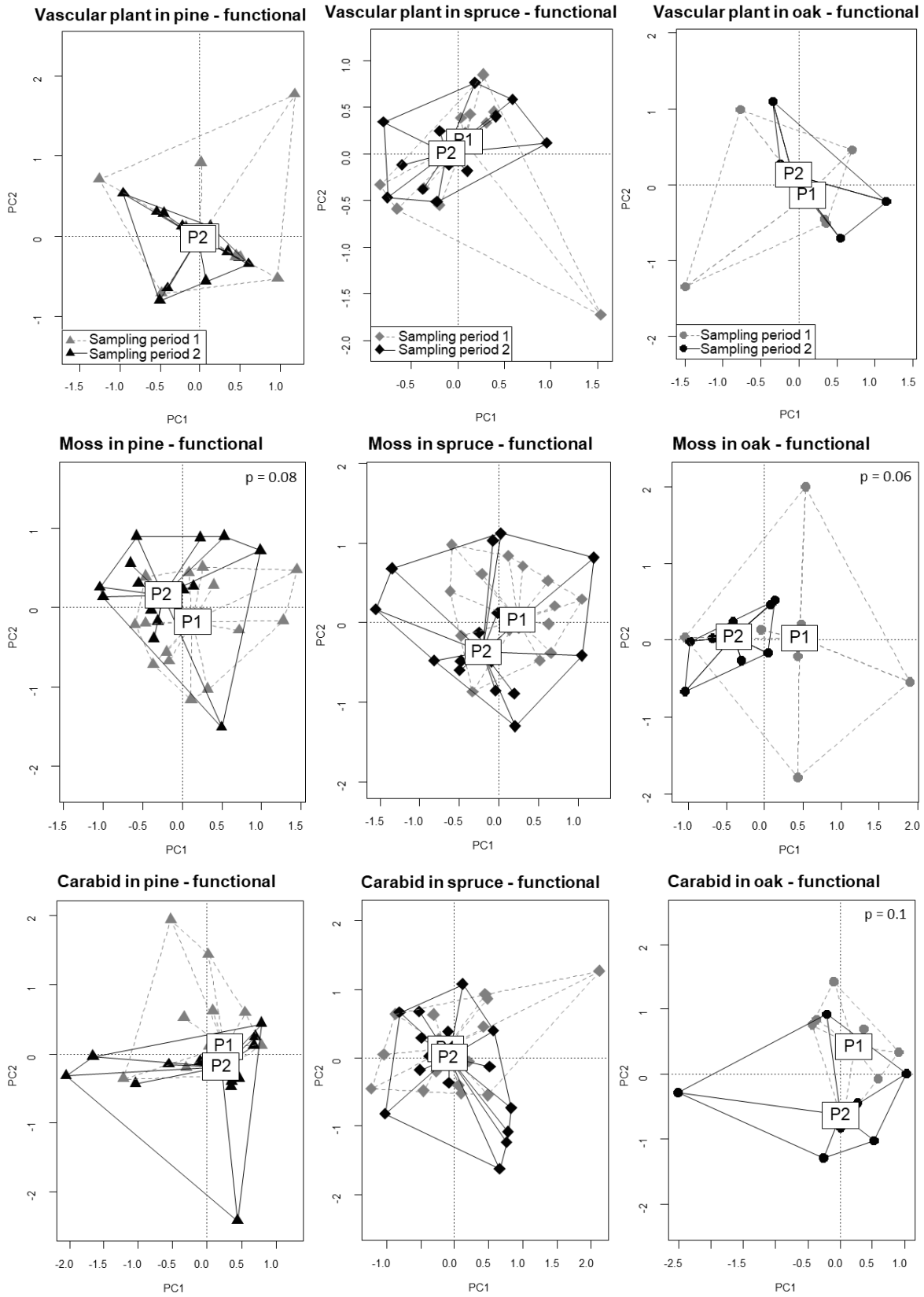


Figure 3.6: Functional trait-based unconstrained RDA ordinations of vascular plant, moss and carabid communities in Scots pine plantations, Sitka spruce plantations and semi-natural oak forests showing samples grouped by sampling period. Variation due to chronosequence location is partialled out. Sample period 1 (P1) is indicated by grey points and dashed lines and sample period 2 (P2) is indicated by black points and solid lines. P1 and P2 boxes indicate centroids of communities for the respective sampling period. Significant and near-significant p values are indicated on plots where applicable.

Winners and losers

Over time, moss, vascular plant and ground active carabid beetle communities in all stand types contained species that changed dominance categories (Table 3.3). For vascular plant and moss communities, there were a greater overall number of species that were losers rather than winners, especially in oak and spruce stands. In pine stands the number of losers and winners were similar for vascular plants, and there were more winners than losers in carabid communities. Carabids also had similar numbers of winners and losers in the spruce and oak plantations. Dominance categories and dominance values for all species in each time period are listed in Appendix 3.3.

Table 3.3: Number of species in each taxonomic group and in each forest type that changed dominance category between Sampling Periods 1 and 2 with percentage of total species in parentheses. Winners were in a higher dominance category and losers were in a lower dominance category during Sampling Period 2.

	VASCULAR PLANTS		**MOSSES**		**CARABIDS**	
	Winners	Losers	Winners	Losers	Winners	Losers
PINE	31 (37%)	30 (36%)	11 (33%)	12 (36%)	18 (40%)	12 (27%)
SPRUCE	11 (16%)	45 (67%)	7 (22%)	17 (53%)	10 (26%)	14 (36%)
OAK	19 (17%)	65 (58%)	2 (7%)	17 (59%)	14 (30%)	14 (30%)

Dispersal-related trait values for winners and losers showed few consistent differences and those of resource-acquisition showed no significant differences (Table 3.4). Vascular plants that had decreased in dominance in oak forests since Sampling Period 1 had significantly lighter seeds than species that had increased in dominance. Dispersal ability of winning and losing moss species in oak forests was near-significantly different, with larger spores amongst species that had decreased in dominance. Seed mass and spore size of winning and losing species were not significantly different in pine or spruce stands. Wing-form of carabid winners and losers showed near-significant differences in pine and spruce forests only. Winners in both forest types were more likely to be winged, whereas species that had decreased in dominance in pine forests were more likely to be dimorphic and those in spruce were more likely to be dimorphic or wingless.

Table 3.4: Differences in trait values between winners and losers. Results display outcomes of Fligner-Killeen tests (continuous traits) and Fisher's exact tests (categorical traits) showing p values and differences in trait values for significant and near-significant tests

	VASCULAR PLANTS				MOSSES				CARABIDS			
	Seed mass		SLA		Spore size		Life-form		Wing-form		Diet	
	p	result	p	result	p	result	p	result	p	result	p	result
PINE	0.57	NS	0.96	NS	0.92	NS	0.28	NS	0.09	Winners winged Losers dimorphic	0.13	NS
SPRUCE	0.55	NS	0.41	NS	0.81	NS	0.38	NS	0.09	Winners winged Losers dimorphic / wingless	0.88	NS
OAK	0.004	Losers lighter	0.90	NS	0.09	Losers larger	0.23	NS	0.74	NA	1	NS

Species with notable changes in dominance values.

Seven species had large changes in dominance values (increase or decrease by 20%) across the taxa, whilst remaining in the dominant category. In spruce forests, there was a steep decline of regenerating Sitka spruce (*P. sitchensis*) over time, with the species going from dominant to uncommon. In oak stands, cover of the fern, *Pteridium aquilinum*, increased and cover of *Rubus fruticosus* decreased over time. The former was a dominant species in both sampling periods but *R. fruticosus* went from being dominant to sub-dominant. *Thuidium tamariscinum* remained a dominant moss species in oak forests during both sampling periods, but with higher cover and frequency during Sampling Period 2 resulting in a much higher dominance value.

In spruce, the carabid species *Pterostichus madidus,* increased from subdominant to dominant between Sample Period 1 and 2 and the reverse happened to the carabid species *Trechus obtusus.* The carabid, *Abax parallelepipedus,* was a dominant species in oak forests during both sampling periods but the dominance value of this species had increased by sampling period two.

Discussion

Is there evidence of biotic homogenisation of communities over a 20-year period?

As predicted, we found some evidence of declines in the metrics of diversity in all forest types. However, contrary to our predictions, there was little evidence of reduced beta dispersion or changes in composition suggesting that the overall effect on communities is subtle and likely being driven by the loss or gain of a few species rather than by a significant degree of turnover or nestedness (Baselga, 2010). Research has found mixed evidence for homogenisation, especially in forest habitats (Baeten et al., 2012; Hester et al., 2019; Keith et al., 2009; Smart et al., 2006). Where homogenisation has been detected, this is generally attributed to major management changes in the forest or surrounding area, e.g. eutrophication, land use or grazing intensification (Keith et al., 2009; Reinecke et al., 2014; Ribeiro-Neto et al., 2016; Rooney et al., 2004). Therefore results are likely study specific, variability in response arising from differences in the time period, habitat and taxa studied (Carvalheiro et al., 2013; Knop, 2016; Ribeiro-Neto et al., 2016; Smart et al., 2006).

Some declines SR, SD and FD were detected, particularly for vascular plant and moss communities in Sitka spruce and Oak. However, overall diversity metrics, and compositional measures largely remained the same across all taxa and forest types, especially in carabid communities. This is in contrast with many other studies which have generally found widespread declines in SR, SD, biomass and abundance across habitats and taxa over a time period ranging from 1930 to 2017 (Alignier, 2018; Carvalheiro et al., 2013; Hallmann et al., 2017; Ross et al., 2012; Seibold et al., 2019). However, evidence suggests changes in diversity depend on the specific time period in question (Carvalheiro et al., 2013; Macgregor et al., 2019) and other long term studies have found that diversity has not changed (Keith et al., 2009), has increased (Reinecke, Klemm and Heinken, 2014) or that different metrics detected opposite patterns over time (Hester et al., 2019; Smart et al., 2006).

Most studies of long-term changes in biodiversity only measured species richness or simply biomass (but see Keith et al., 2009, Ross et al., 2012, Reinecke, Klemm and Heinken, 2014, Hester et al., 2019). However, we took a more detailed approach since compositional changes can occur without changes in richness or abundance and can give further insight into the drivers of change. For example, Pozsgai et al. (2016) found that changes in carabid communities over time could only be detected using multivariate methods and not diversity indices. These changes in all habitat types studied were related to decreasing temperatures and increasing precipitation (Pozsgai et al., 2016) This supports our study, where the only significant change in carabid communities was in taxonomic composition. In addition, due to a prolonged drought during Sampling Period 1, Sampling Period 2 had higher precipitation, and this may have resulted in the observed changes in taxonomic composition (Met Office, 2019).

We found community composition was unchanged in vascular plant and bryophyte communities. Contrary to our study, compositional changes have been detected in forests and eutrophication and canopy closure were thought to be responsible (Keith et al., 2009; Reinecke et al., 2014). These studies took place over a much longer time period (e.g. 45-70) perhaps indicating that our 20-year period may not be long enough to detect significant changes in forest vegetation community composition. Furthermore, we used a different community data transformation method to these studies (Hellinger transformation), since this is recommended to ensure community data meets the assumptions of Euclidean based analyses (Legendre and Gallagher, 2001). However, this can result in a more conservative result if community changes are subtle since it downweights the importance of rare species as well as the most abundant species, potentially explaining why we observed fewer community changes (Legendre and Gallagher, 2001).

Only one diversity metric increased over the sampling period, and this was SD of Vascular plants in Scots pine stands. This change was likely driven by community evenness, since SD, community composition and beta diversity were the same in both sampling periods.

There are few examples of long-term studies in pine forests, though Reinecke, Klemm and Heinken (2014) found a similar trend. However, in their study of German pine forests, the increase in SD was attributed to large changes in composition (driven by nitrogen enrichment), rather than a more even community. Again, Reinecke, Klemm and Heinken (2014) observed these changes over a 45-year period and it is possible that our 20-year study period was not long enough for all vascular plant community changes to be detected.

Interestingly, we found stronger evidence of reduced diversity in oak forests, rather than the conifer forests, particularly for mosses. Long-term studies of moss communities in forested habitats are rare but studies in other habitats have shown that biotic homogenisation has occurred (Ross et al., 2012), though, this varies with habitat type (Ross et al., 2012). In spruce stands, only moss SR declined. Since SR is more sensitive to the loss of rare species than other diversity indices, this indicates a loss of rare species in particular (Morris et al., 2014). In oak stands, on the other hand, both SR and SD declined, and this was the result of losses of both rare and common species. In this study, the oak forests are less intensively managed than the conifers, with conservation rather than timber a primary output. Although the oak forests are of planted origin, the stands are on ancient woodland sites. In addition, limited intervention has led to natural development of these stands. They are also native throughout the geographical range studied, whereas SS are not and SP only in the north. Therefore, these oak forests more closely resemble natural woodland (Peterken, 2019; Schuck et al., 2002). Natural woodlands are likely to support more specialised forest communities (Brockerhoff et al., 2008), and these communities have more specialists which are more vulnerable to change (Sing et al., 2017).

Carabid beetles were the only group to show significant changes in taxonomic composition and this was only in the oak forests, though there was a non-significant trend in the other forest types. However, this was not coupled with any changes in diversity metrics or beta diversity, providing evidence for a shift in species identity rather than biotic homogenisation. In a study of carabid communities in a range of sites including heath, grassland, pasture

and woodland, Brooks et al. (2012) found forests and hedgerows to be among the only habitats in the UK with stable populations over a 10-year period. Other long-term studies of carabid communities have also found overall declining diversity trends in open habitats (Homburg et al., 2019; Pozsgai et al., 2016; Pozsgai and Littlewood, 2014; van Noordwijk et al., 2017). This suggests, along with our results, that carabid diversity in forest habitats may be less vulnerable to local extinction over time than in open habitats.

Winners and losers

Overall there were greater numbers of losers than winners, reflecting the overall trend of declining diversity found in other studies (Alignier, 2018; Hester et al., 2019; Pozsgai and Littlewood, 2014). Greater numbers of losers were expected since, in general, fewer species are likely to benefit from human activities over time (McKinney and Lockwood, 1999). However, contrary to our prediction, we did not find differences in the functional traits of winners and losers. Although there is evidence from other studies that some plant trait values change over the long-term (e.g. pollination mechanism, tolerance to grazing and Ellenburg values), other traits, including dispersal-related traits, have remained the same despite changes in habitat conditions and climate (Alignier, 2018; Wiegmann and Waller, 2006). For insects on the other hand, Gámez-Virués et al. (2015) found that species with specialised diets were negatively affected by landscape simplification and intensification. These findings likely differ from ours because their study included insect orders which contain species with highly specialised, species-specific relationships with plant food sources (e.g. non-carabid Coleoptera, Hemiptera and Lepidoptera), whereas carabid beetles generally do not exhibit this degree of diet specialisation.

Notably, all of the species in this study which increased their dominance over the 20-year period were considered habitat generalists since they are not restricted to forests (Grime, Hodgson and Hunt, 1988; Pakeman, Le Duc and Marrs, 2000; Luff 2007; Atherton *et al* 2010). These species are able to use the surrounding habitat “matrix” (this being the surrounding non-forested land cover in this case) and so are considered less vulnerable to

local extinction (Sweaney *et al.*, 2015). Supporting our findings, many other studies have found that generalist species increase in dominance while specialists were less common over time and this has been attributed to changes in climate, important nutrients in the soil, canopy cover and grazing pressure (Alignier, 2018; Hester et al., 2019; Keith et al., 2009; Pozsgai et al., 2016; Ross et al., 2012). However, many of these studies classified generalists by their habitat preferences rather than strictly functional traits and this would explain why our overall winner and loser functional traits did not reveal the same trend. Therefore, differences in the requirements of winners and losers may be driven by other factors such as habitat specificity, grazing tolerance, activity period or Ellenburg scores (Gámez-Virués et al., 2015; Wiegmann and Waller, 2006). Additionally, species that were lost between sampling periods could have simply been more vulnerable to stochastic processes due to their small population sizes rather than because of vulnerable life-history strategies (Zhang et al., 2016).

Scots pine had no notable changes in dominance of any taxa and trait values of winners and losers were the same. Other studies have not always found this to be the case for pine forests (Reinecke et al., 2014; Wiegmann and Waller, 2006). However, few differences in Scots pine community composition and diversity were detected overall and so the similar dominance structure in pine stands reflects that these communities did not change over the 20-year time period. In contrast, although in Sitka spruce trait values of winners and losers were also similar there were several notable changes in species dominance. The carabid *Trechus obtusus* declined in abundance. This is a generalist predator and so does not require specialist resources, it is small (3.8 mm) and is incapable of flight (Luff, 2007) so is likely to be immobile and therefore more vulnerable to habitat change and fragmentation (Den Boer, 1990; McKinney and Lockwood, 1999). There was a corresponding increase in dominance of *Pterostichus madidus*. This was found to be due to a large increase in abundance in a single study plot (5.1). Since dominance values are based on proportional abundances and proportional frequencies, the decline in *T. obtusus* appeared more notable

than if *P. madidus* was discounted. Discounting changes in *P. madidus* also resulted in a more notable increase in the dominance value of *Abax parallelepipedus* in spruce stands. As previously noted, there was a relative increase in precipitation by Sampling Period 2 (Met Office, 2019). It has been observed that generalist predatory carabids (such as *A. parallelepipedus*) benefit from increased precipitation, and this may explain why this species became more dominant in spruce stands (Pozsgai et al., 2016).

There was a large decline in *Picea sitchensis* in Sitka spruce but, upon further examination, this was found to be almost exclusive to the youngest spruce stands indicating that this change may have been due to inconsistencies in recording between sampling periods. Young spruce saplings were considered canopy trees and so were not included in ground vegetation estimates during Sampling Period 2. However, they may have been included in ground vegetation during Sampling Period 1. This would account for the observed reduction in cover and does not represent a genuine decline in this species. *Calluna vulgaris* showed a notable increase in dominance. However, after accounting for the potential sampling artefact which resulted in a notable decrease in *P. sitchensis* regeneration, the increase in dominance of *Calluna vulgaris* was also no longer notable.

Most of the notable changes in dominance were in oak, as was the only significant trait difference between winners and losers, where vascular plant losers had lighter seeds. We expected that losers would have larger seeds because this could make them more vulnerable to habitat changes due to poor dispersal ability (Lawton, 1994; McKinney and Lockwood, 1999; Virtanen, 2014; Westoby, 1998). Where other long-term studies have explored dispersal ability of taxa, they have usually considered dispersal strategy rather than dispersule size (Alignier, 2018; Rooney et al., 2004; Wiegmann and Waller, 2006) and these have found variable results. Poor dispersal ability is hypothesised to be a disadvantage specifically where habitat reduction and isolation has occurred (den Boer, 1990). Our study was designed to include only forests which were not isolated, and this may have produced conflicting results. Also, since forest cover in the study region is increasing

(Forest Research, 2019), it could be assumed that forest habitat in Great Britain is not becoming reduced and isolated and poor dispersers are, therefore, not more vulnerable overall.

We found the vascular plant *Pteridium aquilinum,* markedly increased in dominance in oak forests. Hester et al. (2019) also found this species increased in dominance in semi-natural native forest types in Scotland, which they attributed to climate change. *P. aquilinum* is recognised as an invasive species (CABI, 2019), which, as an unpalatable, shade-intolerant fern, benefits from increased grazing pressure (Tansley 1939 in Kirby, 2001). McKinney and Lockwood (1999) have stipulated that homogenisation can occur through the exclusion of species from the community as a result of invasive species. Since *P. aquilinum* was already a dominant species in oak forests and mainly increased in cover rather than frequency, this may explain why biotic homogenisation was not more evident from the univariate diversity metrics used. *P. aquilinum* has adaptations allowing it to establish, persist and outcompete other species including light weight and numerous spores, toxicity to grazers, allelopathy and protective underground rhizomes (Grime et al., 1988). Indeed, *P. aquilinum* is known to expand its presence at the expense of other species, especially under grazing pressure (Kirby, 2001), and so may have contributed to the high numbers of 'losers' in this study.

Changes in moss diversity in oak forests may be indirectly related to the increase in dominance of *P. aquilinum*. *Thuidium tamariscinum,* a weft-forming moss, increased in dominance. It is capable of dominating ground vegetation (Atherton et al., 2010) and is associated with relatively shaded woodland floors (Birse, 1958). Although the oak forests did not cast deep shade, the dense understorey created by *P. aquilinum* may have contributed to the shading-out of more light-demanding mosses from the ground flora, such as *Hylocomium splendens* or *Rhytidiadelphus squarrosus,* neither of which were recorded in Sampling Period 2 but were subdominant species during Sampling Period 1.

For carabids, one species was a major driver of change; *A. parallelepipedus* increased over the study period to such as extent that it resulted in near-complete dominance of carabid communities in the oak forest. It also increased in dominance in Sitka spruce and Scots pine forests, though the change was not as notable. There is little information in the literature to explain the increasing dominance of this species among forest plots. However, as suggested in spruce stands, this generalist predator may have benefitted from higher precipitation in Sampling Period 2 compared to Sampling Period 1 when there was a drought (Met Office, 2019; Pozsgai et al., 2016). In addition, Hawes, Stewart and Evans (2002) found that large-bodied carabids, and *A. parallelepipedus* especially, could benefit from high cover of *P. aquilinum* and the deep litter layers formed by this fern due to increased availability of prey items. Other authors have also suggested that deep leaf litter can support carabids indirectly through prey availability (Guillemain et al., 1997; Magura et al., 2005).

Conclusions

In summary, we found limited evidence of taxonomic biotic homogenisation of communities in common forest types in Great Britain, especially in Scots pine forests but also in Sitka spruce. This was not expected since intensification of human land-use is thought to drive biotic homogenisation (Olden et al., 2016, 2004) and the Scots pine and Sitka spruce forests studied here are intensively managed commercial forests, whereas the oak forests, where evidence of biotic homogenisation was stronger, are managed less intensively for conservation purposes. The contrasting results between forest types as well as with other studies could be due to the differing vulnerability of studied taxonomic groups or varying severity of anthropogenic pressures. Moreover, Hester et al. (2019) suggested variability among studies of homogenisation in forest habitats could be due to the structurally complex nature of these habitats and the influence of multiple factors on this structural complexity, including successional stage, management and site history. The vulnerability of the oak forests could reflect that they have more to lose in the first place as habitats of higher value

to biodiversity (Fahy and Gormally, 1998; Sing et al., 2017). Alternatively, oak forests could be more hospitable habitats for the increasingly dominant species in these communities. Certainly, *P. aquilinum* will not thrive in the more closed canopies of mature Sitka spruce and possibly even Scots pine plantations (Grime et al., 1988; Hale et al., 2009). There was little evidence of functional homogenisation based on the traits examined here and this may require further exploration with alternative functional traits or habitat associations. Alternatively, longer time-periods may be required to observe functional changes in forests, since studies reporting significant changes were in different habitats (e.g. Ross et al., 2012, Carvalheiro et al., 2013, Gámez-Virués et al., 2015) and/or covered longer time periods (e.g. Rooney et al., 2004, Ross et al., 2012, Carvalheiro et al., 2013). Further, since the rate of biotic homogenisation is not expected to be constant through time, it is also probable that the number of losses or gains witnessed, and therefore the detection of biotic homogenisation, may depend on the stage in the process at which you begin observations, and the length of time for which you observe (Olden, 2006). Olden (2006) suggested this is because colonisation and extinction do not occur at the same rate and so invasion by generalist species can initially increase diversity and dissimilarity of communities prior to declines. In this study, the main changes were driven by common species already present in communities, as indicated by changes in dominance values. Since this is one of the major processes leading to biotic homogenisation, it was surprising that changes in beta dispersion were not detected where changes in the dominance structure of communities had occurred (Olden et al., 2004).

Chapter 3 Appendices

Appendix 3.1: Locations and characteristics of spruce, pine and oak study plots.

Location	Stand number	Stand Coordinates Sampling Period 1		Stand Coordinates (where replaced) Sampling Period 2		Tree Age at start of Sample Period 1	Tree Age at start of Sample Period 2	% main crop species	Plot elevation (m.a.s.l.)
Scots pine									
Glen Affric	1.1	57.3469	-4.7209			12	32	100	240
	1.2	57.2929	-4.8577			35	55	94	200
	1.3	57.2701	-4.8664			96	116	95	300
	1.4	57.2887	-4.9252	57.2612	-4.8776	238	4	95	190
Glenmore	2.1	57.1520	-3.8975	57.1534	-3.7044	8	11	70	400
	2.2	57.1938	-3.7513			32	52	70	400
	2.3	57.1697	-3.6744			64	84	81	380
	2.4	57.1458	-3.7104	57.1524	-3.7062	165	28	90	430
Thetford	3.1	52.4749	0.7007			18	38	63	60
	3.2	52.7150	1.2512	52.4702	0.7160	37	75	100	30
	3.3	52.4293	0.6849			68	8	80	50
New	4.1	50.8565	-1.6404			26	46	100	50
Forest	4.2	50.8454	-1.5281			49	69	88	30
	4.3	50.8327	-1.5173			66	86	80	20
	4.4	51.3825	-0.7325	50.8449	-1.6848	66	21	68	30
Sitka spruce									
Knapdale	5.1	56.0597	-5.5137			9	29	100	150
	5.2	56.0617	-5.5129	56.0636	-5.5087	24	44	100	160
	5.3	56.0806	-5.3168	56.0822	-5.3289	44	9	86	100
	5.4	56.0625	-5.5099			62	82	82	130
Clunes	6.1	57.0030	-4.8707			8	28	100	180
	6.2	56.9737	-4.9889			28	48	92	80
	6.3	56.9584	-4.9799	56.9971	-4.8880	62	10	95	330
	6.4	57.0003	-4.8840			67	87	100	140
Kielder	7.1	55.1679	-2.4492			6	26	100	320
	7.2	55.1472	-2.4594			23	43	78	260
	7.3	55.1565	-2.5183			57	16	100	280
	7.4	55.1406	-2.4660			69	89	98	310
Glentress	8.1	55.6663	-3.1517			10	30	80	460
	8.2	55.6554	-3.1331	55.6652	-3.1557	28	49	100	380
	8.3	55.6733	-3.1479	55.6707	-3.1466	55	7	100	310
	8.4	55.6203	-3.1051			61	81	100	290
Oak									
Alice Holt	9.2	51.1541	-0.8645			61	82	NA	90
	9.3	51.1623	-0.8520			176	197	NA	70
New	10.2	50.9307	-1.6385			60	81	NA	70
Forest	10.3	50.8379	-1.6145			167	188	NA	20
Taynish	11.2	56.0032	-5.6392			100	121	NA	40
	11.3	56.0079	-5.5916			108	129	NA	50
Beasdale	12.2	56.8974	-5.7674			107	128	NA	80
	12.3	56.7912	-5.7603			127	149	NA	30

Appendix 3.2: Functional trait information

Table a: Vascular plant functional traits

Trait	Levels	Rationale	Literature
Seed mass	Continuous (mg)	Indicates dispersal and reproductive effort. Smaller seeds are expected to be more numerous and disperse over longer distances, improving dispersal ability and increasing the chances of finding suitable habitat.	Kleyer et al., 2008; Westoby, 1998
Specific Leaf Area (SLA)	Continuous (mm^2/mg)	SLA is the surface area per dry mass. It represents the rate of return on investment in photosynthesis and is related to responsiveness to opportunities for grow and growth-rate Low SLA indicates a slow-growing, less competitive species and high SLA allows a flexible and fast response to resource availability and higher competitive ability in a range of conditions	Kleyer et al., 2008; Vendramini et al., 2002; Westoby, 1998; Westoby et al., 2002

Table b: Moss functional traits

Trait	Levels	Rationale	Literature
Spore size	Continuous (µm)	Related to dispersal and reproductive effort. Smaller spores are expected to be more numerous and disperse over longer distances, improving dispersal ability and increasing the chances of finding suitable habitat.	Caners et al., 2013; Lönnell, 2014; Virtanen, 2014
Life-form	Turf Weft Mat Cushion	Refers to the organisation of shoots into colonies and has consequences for resisting stresses (especially low water-stress). Wefts, turfs and cushions are better adapted to prevent water loss than mats and are therefore better able to survive a wider range of conditions.	Bates, 1998; Birse, 1957; Caners et al., 2013; Löbel et al., 2018; Proctor et al., 2007

Table c: Carabid functional traits

Trait	Levels/unit	Rationale	Literature
Wing-form	Winged Wingless Wing-dimorphic	Indicates dispersal ability Winged carabids have better dispersal ability and are expected to be less vulnerable to habitat change/fragmentation	den Boer, 1990; Niemelä, 2001; Shibuya et al., 2014
Diet	Specialist predator Generalist predator Herbivore Omnivore	Represents resource-use and niche-breadth. Generalist predators and omnivores have a broader diet and are expected to survive in a wider range of conditions than specialist predators. Herbivorous species are directly dependent on plant species richness and cover and are expected to be more vulnerable to habitat change.	Aubin et al., 2013; Harvey, 2008; Hunter and Price, 1992; Pedley and Dolman, 2014; Ribera et al., 2001; Spake et al., 2016; Thiele, 1977

Appendix 3.3: Average cover (vascular plants and moss) and summed abundance (carabid) of all species identified during both sampling periods with trait values.

Table a) Vascular plant trait data and average cover. P1 represents sampling period one, P2 represents sampling period two, DC represents dominance category (D is dominant, SD is subdominant, LD is locally dominant, C is common and UC is uncommon) and DV represents dominance value. Shading represents winners and losers, with dark grey representing winners and pale grey representing losers.

			Scots pine						Sitka spruce						Oak					
	Seed		P1			P2			P1			P2			P1			P2		
Species	mass	SLA	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Acer campestre	60.30	11.70	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Acer pseudoplatanus	57.50	16.29	0.00			0.00			0.00			0.01	UC	0.01	0.00			1.16	C	0.70
Agrostis capillaris	0.06	27.65	0.30	UC	0.11	0.53	C	0.31	0.53	C	0.56	0.04	UC	0.03	1.13	SD	4.07	1.53	C	1.40
Agrostis curtisii	1.02	22.00	0.20	UC	0.04	0.00			0.00			0.00			0.00			0.00		
Agrostis gigantea	0.08	30.38	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Agrostis stolonifera	0.03	32.19	0.00			0.93	C	0.41	0.00			0.77	C	1.78	0.38	SD	1.02	1.56	SD	1.90
Agrostis vinealis	0.06	18.50	0.03	UC	0.01	0.00			0.13	C	0.10	0.00			0.13	C	0.23	0.00		
Ajuga reptans	1.47	32.00	0.00			0.00			0.00			0.00			0.19	SD	0.51	0.00		
Anthoxanthum odoratum	0.73	30.03	0.03	UC	0.01	0.08	UC	0.01	0.00			0.16	UC	0.12	0.50	SD	1.81	1.55	SD	1.88
Anthriscus sylvestris	4.04	30.00	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Arrhenatherum elatius	2.77	29.04	0.00			0.00			0.00			0.00			0.13	C	0.23	0.08	UC	0.02
Arum maculatum	33.01	33.10	0.00			0.00			0.00			0.00			0.00			0.02	UC	0.00
Asplenium adiantum nigrum	0.00	NA	0.03	UC	0.01	0.00			0.03	UC	0.01	0.00			0.00			0.00		
Athyrium filix-femina	0.00	12.10	0.00			0.00			0.13	C	0.10	0.02	UC	0.02	0.06	UC	0.06	0.00		
Ballota nigra	0.89	21.25	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Betula pendula	0.16	15.54	0.00			0.42	C	0.19	0.00			0.00			0.00			0.00		
Betula pendula x pubescens	0.16	14.97	0.20	SD	0.18	0.00			0.00			0.00			0.13	C	0.23	0.00		
Betula pubescens	0.16	14.40	1.20	C	0.64	0.07	C	0.03	0.44	C	0.46	0.00			0.06	UC	0.06	0.05	UC	0.01
Blechnum spicant	0.00	10.90	0.27	SD	0.28	0.88	SD	0.79	0.66	SD	1.38	0.38	C	1.19	0.25	SD	0.68	2.42	C	2.21
Brachypodium sylvaticum	3.92	41.32	0.03	UC	0.01	0.00			0.00			0.00			0.13	C	0.23	3.02	SD	3.67
Bromopsis ramosa	6.49	21.35	0.07	UC	0.02	0.00			0.00			0.00			0.44	SD	1.58	0.03	UC	0.01
Bromus diandrus	11.45	68.00	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Bromus hordeaceus	1.81	26.49	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Calluna vulgaris	0.03	10.96	11.37	SD	18.16	8.35	SD	12.38	8.97	LD	11.79	8.20	D	31.82	0.19	SD	0.51	0.56	C	0.51
Caltha palustris	0.98	27.30	0.00			0.18	UC	0.03	0.00			0.00			0.00			0.00		
Cardamine pratensis	0.60	18.20	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Carex arenaria	0.78	13.33	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Carex binervis	1.46	10.60	0.00			0.11	UC	0.02	0.03	UC	0.01	0.05	UC	0.08	0.00			0.00		
Carex dioica	0.65	11.80	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Carex echinata	0.77	15.00	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.09	UC	0.03

			Scots pine						Sitka spruce						Oak					
	Seed		P1			P2			P1			P2			P1			P2		
Species	mass	SLA	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Carex laevigata	1.03	18.80	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Carex nigra	0.76	18.02	0.10	C	0.05	0.00			0.00			0.00			0.00			0.00		
Carex paniculata	0.79	15.22	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Carex pilulifera	1.21	20.60	0.00			0.26	UC	0.08	0.00			0.06	UC	0.10	0.06	UC	0.06	0.17	UC	0.05
Carex remota	0.37	25.75	0.00			0.00			0.00			0.00			0.00			0.13	UC	0.04
Carex spicata	2.50	20.26	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Carex sylvatica	1.62	30.90	0.00			0.00			0.03	UC	0.01	0.00			0.25	SD	0.90	0.61	C	0.37
Castanea sativa	1433	12.50	0.13	UC	0.02	0.00			0.00			0.00			0.00			0.00		
Chrysosplenium oppositifolium	0.04	23.35	0.00			0.00			0.19	UC	0.05	0.00			0.00			0.00		
Circaea lutetiana	2.02	36.70	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Cirsium palustre	1.55	18.00	0.00			0.03	UC	0.00	0.03	UC	0.01	0.04	UC	0.03	0.06	UC	0.06	0.00		
Corylus avellana	691.00	16.50	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Crataegus monogyna	89.70	11.46	0.00			0.00			0.00			0.00			0.00			0.72	SD	0.87
Crataegus x macrocarpa	NA	NA	0.00			0.00			0.00			0.00			0.19	SD	0.51	0.00		
Crepis paludosa	0.63	37.00	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Dactylis glomerata	0.90	24.25	0.00			0.00			0.00			0.00			0.25	SD	0.90	0.59	C	0.36
Deschampsia cespitosa	0.20	14.22	0.90	SD	0.96	0.18	UC	0.03	1.03	C	1.36	0.88	C	2.05	0.19	SD	0.51	1.19	C	0.72
Deschampsia flexuosa	0.23	17.30	10.90	D	21.29	10.97	D	17.89	3.75	SD	6.90	2.42	C	7.52	1.31	SD	5.93	2.08	SD	3.16
Digitalis purpurea	0.07	17.30	0.00			0.00			0.09	C	0.07	0.20	C	0.63	0.06	UC	0.06	0.00		
Dryopteris affinis	0.00	25.54	0.00			0.00			1.09	SD	1.73	0.40	C	0.93	0.13	C	0.23	0.86	C	0.78
Dryopteris carthusiana	0.00	25.10	0.00			0.06	UC	0.01	0.00			0.09	UC	0.15	0.00			0.00		
Dryopteris dilatata	0.00	21.00	0.13	C	0.07	0.08	C	0.04	6.56	D	20.71	2.55	SD	21.80	0.19	SD	0.68	0.78	SD	0.95
Dryopteris x complexa	NA	NA	0.00			0.00			0.06	UC	0.03	0.00			0.31	SD	1.41	0.00		
Empetrum nigrum	1.05	8.40	0.00			0.60	UC	0.18	0.00			0.00			0.00			0.00		
Epilobium angustifolium	0.05	21.00	0.03	UC	0.01	0.04	UC	0.01	0.09	C	0.07	0.00			0.06	UC	0.06	0.00		
Epilobium brunnescens	0.02	NA	0.00			0.00			0.13	UC	0.03	0.00			0.00			0.00		
Epilobium hirsutum	0.12	26.20	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Epilobium palustre	0.09	34.40	0.00			0.03	UC	0.00	0.06	UC	0.03	0.00			0.00			0.00		
Epilobium tetragonum	0.10	15.90	0.00			0.00			0.03	UC	0.01	0.00			0.06	UC	0.06	0.00		
Erica cinerea	0.06	11.10	0.43	SD	0.54	0.00			0.00			1.35	UC	2.10	0.13	C	0.23	0.11	C	0.07
Erica tetralix	0.01	9.10	0.13	C	0.07	0.65	C	0.39	0.53	C	0.56	0.49	UC	0.38	0.00			0.00		
Eriophorum vaginatum	0.91	5.99	0.00			0.38	UC	0.06	0.03	UC	0.01	0.00			0.00			0.00		
Euphorbia amygdaloides	4.15	24.04	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.13	UC	0.04
Fagus sylvatica	140.00	14.30	0.03	UC	0.01	0.03	UC	0.01	0.00			0.00			0.06	UC	0.06	1.02	C	0.62
Festuca gigantea	2.88	27.10	0.00			0.00			0.00			0.00			0.38	SD	1.02	0.00		
Festuca ovina	0.38	16.20	4.67	UC	0.83	0.00			0.00			0.00			0.00			0.16	UC	0.05
Fraxinus excelsior	60.89	13.45	0.00			0.00			0.00			0.00			0.13	C	0.23	0.38	UC	0.11

			Scots pine						Sitka spruce						Oak					
	Seed		P1			P2			P1			P2			P1			P2		
Species	mass	SLA	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Galeopsis tetrahit	4.60	32.96	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Galium aparine	9.54	34.15	0.00			0.00			0.00			0.00			0.00			0.66	C	0.60
Galium palustre	0.91	32.70	0.00			0.00			0.03	UC	0.01	0.00			0.13	C	0.23	0.00		
Galium saxatile	0.65	24.70	0.20	SD	0.18	1.14	SD	1.69	1.44	SD	3.40	0.56	C	1.31	0.38	SD	1.36	0.28	C	0.26
Geranium robertianum	1.51	31.10	0.00			0.00			0.03	UC	0.01	0.00			0.06	UC	0.06	0.11	C	0.07
Geum urbanum	2.45	40.90	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Glechoma hederacea	0.69	34.45	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.03	UC	0.01
Goodyera repens	0.00	7.00	0.07	UC	0.02	0.18	UC	0.05	0.00			0.00			0.00			0.00		
Hedera helix	20.43	12.00	0.07	UC	0.02	0.33	C	0.15	0.00			0.00			0.25	SD	0.90	0.52	SD	0.78
Holcus lanatus	0.43	33.05	0.07	UC	0.02	0.06	UC	0.02	1.41	C	1.85	0.03	UC	0.02	0.19	SD	0.51	0.27	C	0.16
Holcus mollis	0.35	39.95	0.07	UC	0.02	0.43	C	0.19	0.00			1.26	UC	0.98	0.13	C	0.23	0.30	C	0.18
Hyacinthoides non-scripta	5.84	20.30	0.00			0.00			0.00			0.00			0.25	SD	0.90	0.61	SD	0.74
Hypericum perforatum	0.11	22.12	0.03	UC	0.01	0.00			0.00			0.00			0.06	UC	0.06	0.00		
Hypericum pulchrum	0.08	17.60	0.00			0.13	C	0.07	0.00			0.02	UC	0.02	0.06	UC	0.06	0.03	UC	0.01
Ilex aquifolium	29.19	6.50	0.13	C	0.09	0.17	C	0.07	0.03	UC	0.01	0.00			0.56	SD	3.05	1.41	SD	2.14
Juncus bulbosus	0.02	18.62	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Juncus conglomeratus	0.02	4.90	0.00			0.03	UC	0.00	0.03	UC	0.01	0.00			0.00			0.00		
Juncus effusus	0.02	6.76	0.07	UC	0.02	1.07	UC	0.16	1.34	C	1.06	0.16	UC	0.12	0.19	SD	0.51	0.00		
Juncus inflexus	0.03	3.65	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.16	UC	0.05
Juncus squarrosus	0.08	5.83	0.00			0.00			0.09	C	0.07	0.00			0.00			0.00		
Juncus triglumis	0.02	NA	0.07	UC	0.02	0.00			0.00			0.00			0.00			0.00		
Juniperus communis	8.63	5.85	0.33	UC	0.06	0.00			0.00			0.00			0.00			0.00		
Leontodon hispidus	0.99	24.64	0.00			0.00			0.06	UC	0.02	0.00			0.00			0.00		
Lonicera periclymenum	5.97	14.20	0.07	UC	0.02	1.13	C	0.67	0.00			0.00			0.44	SD	2.37	1.22	C	1.11
Luzula multiflora	0.37	22.70	0.07	UC	0.02	0.03	UC	0.00	0.03	UC	0.01	0.00			0.00			0.00		
Luzula pilosa	0.93	25.10	0.00			0.14	C	0.06	0.03	UC	0.01	0.13	UC	0.19	0.00			0.05	UC	0.01
Luzula sylvatica	0.70	16.45	0.00			0.00			0.47	UC	0.25	0.00			0.06	UC	0.06	0.00		
Lycopodium clavatum	0.00	21.79	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Lysimachia nemorum	0.35	30.20	0.00			0.00			0.00			0.00			0.19	SD	0.51	0.08	UC	0.02
Melampyrum pratense	5.88	26.29	0.07	UC	0.02	0.12	C	0.05	0.00			0.00			0.19	SD	0.51	0.63	SD	0.76
Melica uniflora	2.77	39.60	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.17	UC	0.05
Mercurialis perennis	4.80	26.40	0.00			0.00			0.00			0.00			0.19	C	0.34	0.63	UC	0.19
Milium effusum	1.14	33.35	0.00			0.00			0.00			0.00			0.00			0.05	UC	0.01
Moehringia trinervia	0.21	34.30	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Molinia caerulea	0.74	21.44	4.83	SD	8.58	9.92	D	13.24	0.78	C	0.62	0.51	UC	0.79	0.56	C	1.02	4.22	SD	5.13
Oreopteris limbosperma	0.00	13.40	0.00			0.00			0.19	C	0.15	0.63	UC	0.98	0.06	UC	0.06	1.25	C	0.76
Oxalis acetosella	0.97	61.46	0.47	C	0.25	0.53	C	0.32	4.53	SD	10.72	3.55	SD	16.55	0.94	SD	5.93	2.97	SD	6.32
Parnassia palustris	0.03	23.95	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		

			Scots pine						Sitka spruce						Oak					
	Seed		P1			P2			P1			P2			P1			P2		
Species	mass	SLA	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Phragmites australis	0.13	15.70	0.00			0.04	UC	0.01	0.00			0.00			0.00			0.00		
Picea abies	6.42	3.32	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Picea sitchensis	0.02	6.30	0.00			0.00			9.56	D	27.66	0.40	UC	0.62	0.00			0.00		
Pinus sylvestris	7.11	4.97	2.13	SD	4.17	0.05	C	0.02	0.00			0.00			0.00			0.00		
Plantago lanceolata	1.81	19.65	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Plantago major	0.25	23.31	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Poa annua	0.21	33.92	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Poa nemoralis	0.18	49.90	0.00			0.00			0.16	UC	0.08	0.00			0.00			0.00		
Poa trivialis	0.20	30.00	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Polypodium interjectum	0.00	15.19	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Polypodium vulgare	0.00	12.35	0.07	UC	0.02	0.00			0.00			0.00			0.13	C	0.23	0.00		
Potentilla erecta	0.47	23.51	0.00			0.74	SD	0.66	0.00			0.14	UC	0.11	0.00			1.58	SD	1.92
Potentilla sterilis	0.54	24.60	0.00			0.00			0.03	UC	0.01	0.00			0.13	C	0.23	0.00		
Potentilla x mixta	NA	NA	0.37	SD	0.59	0.00			0.19	SD	0.30	0.00			0.31	SD	1.13	0.00		
Primula vulgaris	1.12	28.60	0.03	UC	0.01	0.00			0.00			0.00			0.19	SD	0.51	0.00		
Prunella vulgaris	0.67	31.10	0.00			0.00			0.00			0.00			0.13	C	0.23	0.27	C	0.24
Prunus spinosa	145.20	14.30	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Pteridium aquilinum	0.00	20.05	15.23	SD	29.75	17.01	D	30.27	0.31	UC	0.08	0.59		0.45	2.50	D	13.55	23.72	D	43.25
Quercus petraea x robur	NA	NA	0.00			0.00			0.00			0.00			0.19	SD	0.51	0.00		
Quercus robur	3204.5	14.24	0.07	UC	0.02	0.09	C	0.04	0.00			0.00			0.69	C	1.24	0.45	SD	0.55
Ranunculus acris	1.79	22.50	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.08	UC	0.02
Ranunculus ficaria	1.58	29.43	0.00			0.08	UC	0.01	0.00			0.00			0.00			0.00		
Ranunculus repens	1.92	23.00	0.00			0.28	UC	0.08	0.03	UC	0.01	0.00			0.06	UC	0.06	0.28	C	0.26
Rhododendron ponticum	0.06	6.80	0.00			0.00			0.00			0.00			0.00			0.36	C	0.22
Ribes nigrum	0.86	20.65	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Rosa arvensis	15.36	22.05	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Rosa canina	15.76	13.09	0.00			0.00			0.00			0.00			0.00			0.31	UC	0.09
Rubus fruticosus	2.49	15.10	0.13	C	0.09	0.52	C	0.38	0.09	C	0.07	0.15	UC	0.23	4.06	D	22.02	1.48	SD	1.80
Rumex acetosella	0.36	24.80	0.03	UC	0.01	0.33	UC	0.05	0.00			0.00			0.00			0.00		
Sagina procumbens	0.02	19.25	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Salix x smithiana	NA	NA	0.20	UC	0.04	0.00			0.44	UC	0.12	0.00			0.00			0.00		
Scutellaria minor	0.18	37.17	0.00			0.00			0.00			0.00			0.13	C	0.23	0.00		
Silene dioica	0.78	37.72	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Solanum dulcamara	1.54	32.10	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Sorbus aucuparia	3.50	14.03	0.17	SD	0.15	0.23	SD	0.20	0.09	C	0.07	0.06	UC	0.10	0.25	SD	0.90	0.52	SD	0.63
Sorbus intermedia	43.95	19.44	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Stachys sylvatica	1.42	44.70	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Stellaria holostea	2.83	26.80	0.00			0.00			0.00			0.00			0.13	C	0.23	1.03	C	0.94

			Scots pine						Sitka spruce						Oak					
	Seed		P1			P2			P1			P2			P1			P2		
Species	mass	SLA	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Stellaria media	0.38	47.00	0.00			0.03	UC	0.00	0.00			0.00			0.00			0.00		
Stellaria neglecta	0.92	64.10	0.00			0.00			0.00			0.02	UC	0.01	0.00			0.00		
Stellaria uliginosa	0.06	33.60	0.00			0.00			0.00			0.04	UC	0.03	0.00			0.00		
Succisa pratensis	1.37	17.02	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Taraxacum species	0.61	20.47	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Teucrium scorodonia	0.91	28.23	0.03	UC	0.01	0.00			0.00			0.00			0.19	SD	0.51	0.81	UC	0.25
Trientalis europaea	0.64	44.84	0.10	UC	0.04	0.02	UC	0.00	0.00			0.00			0.00			0.00		
Tsuga heterophylla	1.75	76.00	0.03	UC	0.01	0.00			0.00			0.00			0.00			0.00		
Ulex europaeus	6.20	8.50	0.00			0.08	UC	0.01	0.00			0.00			0.00			0.00		
Urtica dioica	0.15	26.95	0.00			0.00			0.94	UC	0.25	0.06	UC	0.05	0.06	UC	0.06	0.08	UC	0.02
Vaccinium myrtillus	0.26	18.34	5.73	SD	10.18	10.18	D	15.10	2.44	SD	7.05	0.92	SD	6.44	2.31	D	8.36	4.47	SD	6.79
Vaccinium vitis-idaea	0.27	6.94	2.07	SD	2.20	4.65	C	3.45	0.00			0.00			0.00			0.00		
Valeriana officinalis	0.96	29.10	0.00			0.08	UC	0.01	0.00			0.00			0.00			0.00		
Veronica chamaedrys	0.19	29.43	0.00			0.00			0.00			0.00			0.19	SD	0.51	0.00		
Veronica montana	0.38	36.08	0.00			0.00			0.00			0.00			0.13	C	0.23	0.14	C	0.09
Veronica officinalis	0.11	28.28	0.00			0.09	UC	0.03	0.03	UC	0.01	0.04	UC	0.03	0.00			0.03	UC	0.01
Vicia sativa	26.85	21.20	0.03	UC	0.01	0.02	UC	0.00	0.00			0.00			0.00			0.00		
Viola palustris	0.63	36.50	0.00			0.00			0.00			0.00			0.06	UC	0.06	0.00		
Viola riviniana	1.11	25.20	0.03	UC	0.01	0.16	UC	0.05	0.09	C	0.07	0.16	UC	0.24	0.63	SD	3.95	1.42	SD	3.02

Table b) Moss trait data and average cover. P1 represents sampling period one, P2 represents sampling period two, DC represents dominance category (D is dominant, SD is subdominant, LD is locally dominant, C is common and UC is uncommon) and DV represents dominance value. Shading represents winners and losers, with dark grey representing winners and pale grey representing losers.

			Scots pine						Sitka spruce						Oak					
		Life	P1			P2			P1			P2			P1			P2		
Species	spores	form	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Aulacomnium palustre	12.5	turf	0.00			0.03	UC	0.01	0.00			0.00			0.00			0.00		
Atrichum undulatum	18	turf	0.00			0.00			0.00			0.00			0.13	C	0.58	0.00		
Brachythecium rutabulum	20	mat	0.37	C	0.64	0.00			0.00			0.00			0.06	UC	0.15	0.08	UC	0.10
Bryum capillare	13.5	turf	0.00			0.00			0.00			0.00			0.06	UC	0.15	0.00		
Campylopus flexuosus	15	turf	0.00			0.09	C	0.14	0.03	UC	0.01	0.16	UC	0.07	0.00			0.00		
Dicranella heteromalla	14.5	turf	0.33	SD	1.03	0.00			0.00			0.00			0.13	C	0.58	0.00		
Dicranoweisia cirrata	16	cushion	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Dicranum majus	20	turf	0.37	C	0.97	0.09	C	0.14	1.41	SD	2.26	1.48	C	2.01	0.38	SD	4.35	0.64	SD	3.28
Dicranum scoparium	17	turf	1.67	SD	9.53	0.80	SD	4.16	3.34	SD	8.96	1.65	SD	3.35	0.25	SD	2.32	0.59	SD	2.28
Eurhynchium striatum	14	weft	0.00			0.03	UC	0.01	0.00			0.00			0.31	SD	3.63	1.23	C	3.16
Fissidens taxifolius	12.5	turf	0.03	UC	0.01	0.00			0.06	UC	0.02	0.00			0.06	UC	0.15	0.00		
Hylocomium splendens	15.5	weft	10.97	D	38.58	10.27	D	42.68	0.03	UC	0.01	0.20	C	0.18	0.69	SD	6.39	0.00		
Hypnum andoi	21	mat	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Hypnum cupressiforme	16	mat	0.30	SD	1.06	0.58	UC	0.30	0.25	C	0.18	0.35	UC	0.08	0.25	SD	2.32	0.05	UC	0.06
Hypnum jutlandicum	14	mat	1.47	SD	6.45	1.69	SD	5.27	5.38	D	11.52	2.74	SD	6.82	0.13	C	0.58	0.00		
Kindbergia praelonga	12	weft	0.37	SD	1.29	1.67	C	3.46	3.03	SD	7.58	4.59	D	12.44	0.50	SD	8.13	0.69	SD	3.52
Leucobryum glaucum	18	cushion	0.00			0.00			0.03	UC	0.01	0.00			0.19	SD	1.31	0.13	UC	0.16
Mnium hornum	30.5	turf	0.07	UC	0.06	0.00			1.91	SD	4.09	2.12	SD	4.31	0.19	SD	1.31	0.20	UC	0.26
Plagiomnium undulatum	28	turf	0.00			0.00			0.13	UC	0.02	0.00			0.31	SD	3.63	0.00		
Plagiothecium undulatum	12.5	mat	1.77	SD	6.21	1.20	SD	4.37	9.47	D	25.37	7.12	D	24.13	0.00			0.03	UC	0.04
Pleurozium schreberi	15	weft	2.47	SD	9.76	2.34	SD	8.52	2.63	SD	3.28	0.69	UC	0.47	0.25	SD	1.74	0.52	SD	1.98
Polytrichastrum formosum	14	turf	0.03	UC	0.01	0.63	C	1.30	1.72	C	1.84	0.25	UC	0.17	0.19	SD	1.31	0.36	UC	0.46
Polytrichum commune	10	turf	0.93	SD	3.28	1.48	SD	5.37	5.19	D	10.19	4.48	D	11.13	0.38	SD	3.48	0.89	SD	4.57
Polytrichum juniperinum	9	turf	0.07	UC	0.06	0.00			0.00			0.00			0.00			0.00		
Pseudoscleropodium purum	14	weft	0.83	SD	2.93	2.98	SD	12.37	0.78	C	0.70	0.05	UC	0.02	0.13	C	0.58	0.33	C	0.84
Ptilium crista-castrensis	12	weft	0.00			1.14	C	1.78	0.00			0.00			0.00			0.23	UC	0.30
Pseudotaxiphyllum elegans	12	mat	0.00			0.00			0.69	UC	0.37	0.00			0.00			0.00		
Racomitrium lanuginosum	10	turf	0.17	UC	0.15	0.00			0.00			0.00			0.06	UC	0.15	0.00		
Rhytidiadelphus loreus	16	weft	1.20	SD	3.69	0.30	SD	0.78	2.28	SD	3.67	6.20	D	16.80	0.63	SD	5.81	2.16	SD	11.05
Rhytidiadelphus squarrosus	15	mat	0.13	C	0.23	0.40	UC	0.42	3.34	SD	5.97	0.38	C	0.42	0.25	SD	2.32	0.00		
Rhytidiadelphus triquetrus	17.5	weft	1.03	C	2.27	0.07	UC	0.07	0.00			0.00			0.13	C	0.58	0.77	C	1.96
Sphagnum capillifolium	25.5	turf	1.40	C	3.08	0.04	UC	0.02	2.25	C	2.41	0.63	UC	0.42	0.44	C	2.03	0.05	UC	0.06
Sphagnum denticulatum	31.5	turf	0.60	C	1.06	0.00			1.91	SD	2.72	0.00			0.00			0.00		
Sphagnum fallax/flexuosum	28.5	turf	0.00			0.17	UC	0.09	0.28	UC	0.15	0.45	UC	0.19	0.00			0.00		
Sphagnum fimbriatum	26.5	turf	0.00			0.00			0.00			0.47	UC	0.21	0.00			0.00		

			Scots pine						Sitka spruce						Oak					
		Life	P1			P2			P1			P2			P1			P2		
Species	spores	form	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV	cover	DC	DV
Sphagnum girgensohnii	23.5	turf	0.00			0.29	UC	0.15	0.00			0.49	UC	0.11	0.00			0.00		
Sphagnum palustre	29	turf	0.20	C	0.26	0.90	C	1.40	0.03	UC	0.01	0.40	UC	0.18	0.06	UC	0.15	0.00		
Sphagnum quinquefarium	23.5	turf	0.00			0.04	UC	0.02	0.00			0.96	UC	0.43	0.00			0.00		
Sphagnum rubellum	25.5	turf	0.00			0.08	UC	0.04	0.00			0.00			0.00			0.00		
Sphagnum subnitens	28	turf	0.00			0.78	C	1.22	0.00			0.44	UC	0.30	0.13	C	0.58	0.23	UC	0.30
Tetraphis pellucida	11	turf	0.00			0.00			0.03	UC	0.01	0.00			0.00			0.00		
Thuidium tamariscinum	16	weft	2.80	C	7.39	1.89	SD	5.90	4.84	D	8.65	4.96	D	15.70	2.81	D	45.72	7.31	D	65.60

Table c) Carabid trait data and summed abundance (standardised by trap day and rounded up to the nearest whole number). P1 represents sampling period one, P2 represents sampling period two, DC represents dominance category (D is dominant, SD is subdominant, LD is locally dominant, C is common and UC is uncommon) and DV represents dominance value. Shading represents winners and losers, with dark grey representing winners and pale grey representing losers.

			Scots pine						Sitka spruce						Oak					
	Wing		P1			P2			P1			P2			P1			P2		
Species	form	Diet	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV
Abax parallelepipedus	wingless	specialist predator	1139	D	32.61	1274	D	48.89	343	D	20.22	543	D	33.08	4613	D	60.59	1941	D	86.92
Agonum fuliginosum	dimorphic	generalist predator	1	UC	0.00	0			50	C	0.68	1	UC	0.01	0			5	UC	0.03
Agonum nigrum	winged	generalist predator	0			0			0			0			0			1	UC	0.01
Amara communis	winged	herbivore	0			14	UC	0.06	0			0			0			0		
Amara lunicollis	winged	herbivore	0			1	UC	0.00	0			0			0			0		
Badister bullatus	winged	specialist predator	0			0			0			0			1	UC	0.00	1	UC	0.01
Bembidion lampros	dimorphic	generalist predator	0			0			0			0			1	UC	0.00	0		
Bembidion mannerheimii	wingless	generalist predator	0			3	UC	0.02	0			1	UC	0.01	0			3	UC	0.02
Bradycellus harpalinus	winged	omnivore	0			0			2	UC	0.01	1	UC	0.01	0			0		
Bradycellus ruficollis	dimorphic	omnivore	0			0			1	UC	0.00	0			0			0		
Bradycellus sharpi	dimorphic	omnivore	0			0			0			0			0			1	UC	0.01
Calathus fuscipes	wingless	generalist predator	2	UC	0.01	0			0			0			0			0		
Calathus melanocephalus	dimorphic	generalist predator	3	UC	0.01	0			0			0			0			0		
Calathus micropterus	wingless	generalist predator	222	C	3.63	47	SD	1.41	296	D	13.42	143	SD	5.80	1	UC	0.00	0		
Calathus rotundicollis	dimorphic	generalist predator	16	C	0.33	2	UC	0.01	49	C	0.67	0			2	C	0.01	1	UC	0.01
Carabus arvensis	wingless	generalist predator	28	C	0.23	1	UC	0.02	0			0			20	SD	0.13	0		
Carabus glabratus	wingless	generalist predator	172	SD	5.63	64	SD	2.19	133	SD	4.82	42	C	1.29	10	C	0.03	8	UC	0.05
Carabus granulatus	dimorphic	generalist predator	0			1	UC	0.00	0			0			1	UC	0.00	4	UC	0.02
Carabus nemoralis	wingless	generalist predator	164	C	3.35	23	C	0.30	1	UC	0.00	0			23	SD	0.19	1	UC	0.01
Carabus problematicus	wingless	generalist predator	158	SD	7.76	35	SD	1.05	192	SD	10.45	134	SD	6.11	85	SD	0.84	16	C	0.27
Carabus violaceus	wingless	generalist predator	237	SD	11.63	74	SD	3.77	136	SD	6.78	65	SD	3.98	448	SD	4.41	90	SD	2.51
Cychrus caraboides	wingless	specialist predator	49	SD	1.80	15	SD	0.45	34	SD	1.39	24	SD	1.23	12	SD	0.12	7	SD	0.20
Dicheirotrichus placidus	winged	omnivore	0			0			7	UC	0.03	2	UC	0.01	0			0		

			Scots pine						Sitka spruce						Oak					
	Wing		P1			P2			P1			P2			P1			P2		
Species	form	Diet	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV
Harpalus laevipes	winged	herbivore	0			1	UC	0.00	0			0			0			0		
Harpalus latus	winged	herbivore	0			1	UC	0.00	0			4	UC	0.04	0			0		
Leistus ferrugineus	winged	generalist predator	2	UC	0.01	0			0			0			0			0		
Leistus rufomarginatus	winged	specialist predator	1	UC	0.00	1	UC	0.00	0			1	UC	0.01	1	UC	0.00	0		
Leistus spinibarbis	winged	specialist predator	2	C	0.02	0			0			0			0			0		
Leistus terminatus	dimorphic	specialist predator	96	SD	2.75	16	SD	0.41	20	SD	1.00	19	C	0.39	0			2	C	0.02
Loricera pilicornis	winged	specialist predator	0			0			1	UC	0.00	0			1	UC	0.00	3	C	0.05
Nebria brevicollis	winged	specialist predator	5	UC	0.02	4	C	0.05	11	UC	0.10	18	UC	0.18	78	SD	0.64	58	SD	1.61
Nebria rufescens	winged	generalist predator	0			2	UC	0.02	4	UC	0.04	1	UC	0.01	0			0		
Notiophilus biguttatus	dimorphic	specialist predator	45	SD	1.47	7	C	0.09	17	C	0.39	9	C	0.18	11	SD	0.11	1	UC	0.01
Notiophilus germinyi	dimorphic	specialist predator	0			2	UC	0.02	0			0			0			0		
Notiophilus palustris	dimorphic	specialist predator	3	C	0.02	3	UC	0.03	0			0			0			0		
Notiophilus rufipes	winged	specialist predator	7	C	0.09	6	UC	0.03	3	UC	0.03	2	UC	0.02	5	C	0.02	0		
Oxypselaphus obscurus	wingless	generalist predator	1	UC	0.00	5	UC	0.02	0			0			0			0		
Patrobus assimilis	wingless	generalist predator	0			0			6	C		0			0			0		
Platyderus depressus	dimorphic	NA	0			0			0			1			0			0		
Platynus assimilis	winged	generalist predator	0			5	UC	0.02	0	C	0.08	0			0			0		
Poecilus cupreus	winged	omnivore	1	UC	0.00	0			0			1	C	0.01	0			0		
Poecilus versicolor	winged	specialist predator	0			4	UC	0.02	0			3	UC	0.02	0			0		
Pterostichus adstrictus	winged	generalist predator	0			17	UC	0.07	0			1	UC	0.01	0			1	UC	0.01
Pterostichus aethiops	wingless	generalist predator	0			4	UC	0.02	0			1	UC	0.01	0			2	UC	0.01
Pterostichus cristatus	wingless	generalist predator	0			0			0			0			0			1	UC	0.01
Pterostichus diligens	dimorphic	specialist predator	0			4	UC	0.03	6	UC	0.03	0			0			2	C	0.02
Pterostichus madidus	wingless	generalist predator	357	C	14.60	627	D	26.75	155	SD	7.03	511	D	36.32	2311	D	30.35	107	SD	3.59

			Scots pine						Sitka spruce						Oak					
			P1			P2			P1			P2			P1			P2		
Species	Wing form	Diet	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV	Abund	DC	DV
Pterostichus melanaris	dimorphic	specialist predator	66	SD	0.81	2	UC	0.01	23	UC	0.21	10	UC	0.05	38	SD	0.31	0		
Pterostichus niger	winged	generalist predator	242	SD	8.91	95	SD	4.44	227	D	9.26	102	SD	5.69	202	SD	1.99	29	SD	0.81
Pterostichus nigrita	winged	generalist predator	0			1	SD	0.00	1	UC	0.00	1	UC	0.01	23	SD	0.15	1	UC	0.01
Pterostichus oblongopunctatus	winged	generalist predator	17	C	0.28	71	C	1.20	10	C	0.18	25	UC	0.38	2	UC	0.00	1	UC	0.01
Pterostichus rhaeticus	winged	generalist predator	0			14	UC	0.12	0			4	UC	0.06	7	UC	0.01	5	C	0.06
Pterostichus strenuus	dimorphic	specialist predator	1	UC	0.00	8	UC	0.07	1	UC	0.00	1	UC	0.01	0			4	UC	0.02
Stomis pumicatus	wingless	generalist predator	0			5	UC	0.04	0			3	UC	0.05	0			0		
Synuchus vivalis	dimorphic	generalist predator	0			0			0			0			1	UC	0.00	0		
Trechus obtusus	wingless	generalist predator	140	SD	4.01	195	SD	8.31	391	D	23.04	124	SD	5.06	24	C	0.08	110	SD	3.69
Trechus rubens	winged	generalist predator	0			3	UC	0.03	10	C	0.14	1	UC	0.01	0			3	C	0.03

Chapter 4

Planted forests support a diverse spider fauna and species of conservation concern

Introduction

Spiders are abundant and widely distributed generalist predaceous arthropods which play important functional roles in terrestrial ecosystems (Nyffeler and Birkhofer, 2017). They are important in the control and stabilisation of populations of the species they prey on, including collembola and centipedes, as well as important pest species such as aphids, lepidoptera and coleoptera (Marc and Canard, 1997; Michalko et al., 2019a, 2019b; Nyffeler and Birkhofer, 2017). Spiders also provide a source of food for other species, including birds, lizards and small mammals (Askenmo et al., 1977; Churchfield et al., 1991; Gunnarsson, 2007; Schoener and Spiller, 1987). Since spiders are ubiquitous, generalist predators, they have been thought to be less sensitive to environmental changes as a taxa (Clavel et al., 2011). However, it is now understood that many spider species have specific microhabitat requirements making them vulnerable to habitat change (Huang et al., 2014; Marc and Canard, 1997; Ziesche and Roth, 2008). Although there is a lack of data on this taxon globally, the IUCN red list indicates over half of all spider species assessed to be at least near threatened (IUCN redlist, n.d.). Further, a recent review of the conservation status of spiders in Britain found that one fifth of all native British spider species are categorised as at least near threatened (Harvey et al., 2017). A similar assessment in Germany identified around 45% of all spider species as at least extremely rare or near threatened (Blick et al., 2016). This suggests that spiders are threatened globally and that improving our understanding of their ecology and conservation should be a priority.

Spiders are particularly abundant in forest ecosystems and they play important roles in these food webs (Castro and Wise, 2010; Nyffeler and Birkhofer, 2017). However, global deforestation and expansion of intensively-managed plantation forests threaten forests and their communities (Carnus et al., 2006; FAO, 2015). Conversion to plantation forest in particular can result in simplified or altered forest structure and disrupts natural forest dynamics (Brockerhoff et al., 2008; Carnus et al., 2006; Lindenmayer and McCarthy, 2002). This is expected to affect spider communities since they are known to be strongly affected

by forest structure, specifically vegetation and litter. For example, studies have demonstrated that spiders are sensitive to changes in vegetation cover and structure (Maleque et al., 2009; Oxbrough et al., 2010, 2005; Uetz, 1991; Ziesche and Roth, 2008) as well as leaf or needle litter type, cover and depth (Oxbrough et al., 2005; Ziesche and Roth, 2008). Vegetation and litter structure is important for spiders for many reasons (Uetz, 1991). For example, web-building spiders rely on complex structure for web anchor points, active spiders use all vegetation layers to hunt and all spiders use vegetation structure to conduct vibrations as a method of communication and prey detection (Bultman and Uetz, 1982; Uetz, 1991). Vegetation and litter structure also affect the microclimate and its stability, as well as availability of shelter from predators, both of which are important for survival (Uetz, 1979). In addition, high cover and diversity of vegetation and litter is thought to increase richness and abundance of prey (Bultman and Uetz, 1982; Roberts, 1993; Uetz, 1979). If forest structure can have an impact on spider community composition, it follows, then, canopy tree species (Barsoum et al., 2014; Gallé et al., 2018; Oxbrough et al., 2005) and development stage (Neuvonen et al., 2012; Oxbrough et al., 2005) also affect forest spider communities, and these are key parameters that are altered under differing forest management approaches (Huang et al., 2014; Pinzon et al., 2012). This is particularly true in plantations, which typically differ the most from natural forests, usually with simplified structure, development and different canopy species (Brockerhoff et al., 2008; Carnus et al., 2006; Lindenmayer and McCarthy, 2002).

It is, therefore, important to develop an understanding of how forest management, in particular plantations, influence spider communities. This is especially true in regions where natural forest cover has been drastically reduced and replaced with commercial plantation forests and where these now make up a large proportion of the forest estate (Bremer and Farley, 2010; O'Callaghan et al., 2017; Quine and Humphrey, 2010). This is the situation in Great Britain, where roughly 13% of land cover is forest and 77% of this is plantation forest (FOREST EUROPE, 2015). A similar situation can be found in other countries, especially

in Europe where deforestation has been extensive (FOREST EUROPE, 2015). Forests in this context have been found to support the conservation of forest species because the extent of natural, semi-natural or unmanaged forests alone may not be sufficient to provide this service (Brockerhoff et al., 2008). On the other hand, semi-natural forests have been found to support species of conservation concern not typically found in plantation forests in the same region, suggesting that semi-natural forests have a more significant role in the conservation of forest species (Fuller et al., 2014). However, a lack of understanding of the extent of spider declines globally means that the ability of different forest types to support spider species of conservation concern has received little attention overall in the literature. Further, we have little knowledge on the role of plantations in supporting these species.

This study aims to fill this knowledge gap by exploring epigeal spider diversity in common forest plantation types at a range of stages of development. Further, it will also determine the ground vegetation structural features that are responsible for shaping these communities. Finally, the role of these common forest types in supporting species of conservation concern will be explored. This is the largest scale study of spiders within forests in Great Britain both in terms of forest types (Sitka spruce (*Picea sitchensis* (Bong.) Carrière), Scots pine (*Pinus sylvestris* L.) and oak (*Quercus spp.* L.) and geographical range (south England to north Scotland). Indeed, stands dominated by Scots pine as well as forest stands in northern Britain have generally received less attention (but see Barsoum *et al.*, 2014). We predict that forest type (main tree species/stand stage) will be fundamental in determining epigeal spider community composition, species richness, abundance and species diversity through its effects on ground vegetation structure and litter depth. Stands with higher ground vegetation cover, more structurally complex vegetation cover and deeper litter layers are expected to support more species rich, diverse and abundant spider communities. Forest stands with sparse or simple ground vegetation cover are expected to be species poor and support less abundant spider communities due to a lack of resources. We expect that oak forest stands managed predominately for conservation will be more

important for forest-specialist species of conservation concern than intensively managed plantations.

Methods

Study locations

The study took place in Great Britain using three common forest types, chosen because they represent around 41% of Great Britain's forest cover (Forest Research, 2019). The forests studied were dominated by either Sitka spruce (*Picea sitchensis* (Bong.) Carrière), Scots pine (*Pinus sylvestris* L.) or oak (*Quercus spp.* L.). Sitka spruce and Scots pine are the most common plantation tree species in Great Britain and are managed by clear-cutting and replanting. The oak stands sampled are considered to have semi-natural development despite being of planted origin, since they have been allowed to develop naturally after an intervention, are on ancient woodland sites and predominantly managed for conservation purposes (Peterken, 2019; Schuck et al., 2002). They have therefore developed old-growth features, and many have statutory designations as a result of the quality of forest habitat they provide.

To ensure we represented the key development stages in the forest harvest cycle, stands were selected based on structural development rather than age *per se,* since stands of the same tree species mature at different rates depending on local growing conditions (see Oxbrough et al., 2005). This was done using the structural indicators in Table 4.1 (see Humphrey, Ferris and Quine, 2003). For conifer species, four stages of development are represented, ranging from recently planted to beyond commercial maturity (Table 4.1). This design resulted in 32 stands separated into eight regional clusters (four per tree species), each comprising four stages of forest stand development for conifer (Figure 4.1). For oak, eight stands were selected. However, only one stage of development was studied since newly regenerating oak and very old oak stands are not common in the Britain. As the oak stands were significantly older than most of the conifer stands and most had acquired ecological features of natural old-growth forests (e.g. multiple age classes including large, old trees, an accumulation of deadwood, well developed understorey layers), all oak stands

are referred to as mature. All stands were at least 2.5ha and within large forested areas to reduce the influence of non-forested habitat and study plots were at least 30m from the edge of the stand. Within a regional cluster, stands were matched for similar soils, topography, site history, climate, location and elevation where possible (see Appendix 4.1 for details of stand characteristics). Within cluster distances ranged from 0.15-16 km (median 4.2 km) and distances between clusters were 10-750 km (65-750 km for Scots pine (median 650 km), 65-350 km for Sitka spruce (median 170km) and 60-725 km for Oak (median 635 km)).

Table 4.1: Descriptions of the structural features of different developmental stages used to select forest stands based on Humphrey, Ferris and Quine (2003)

Stand stage	**Tree age (years)**			**Tree height (m)**	**Canopy**	**Understorey**
	Pine	Spruce	Oak			
Pre-thicket	4-21	7-16	NA	2-4	Incomplete	Well developed
Mid-rotation	28-46	26-30	NA	10-20 m	Closed	None
Mature	52-75	43-49	NA	20-25 m	Closed	Some
Over-mature*	84-116	81-89	81-197	>25 m	Re-opening	Well-developed

** referred to as mature in oak*

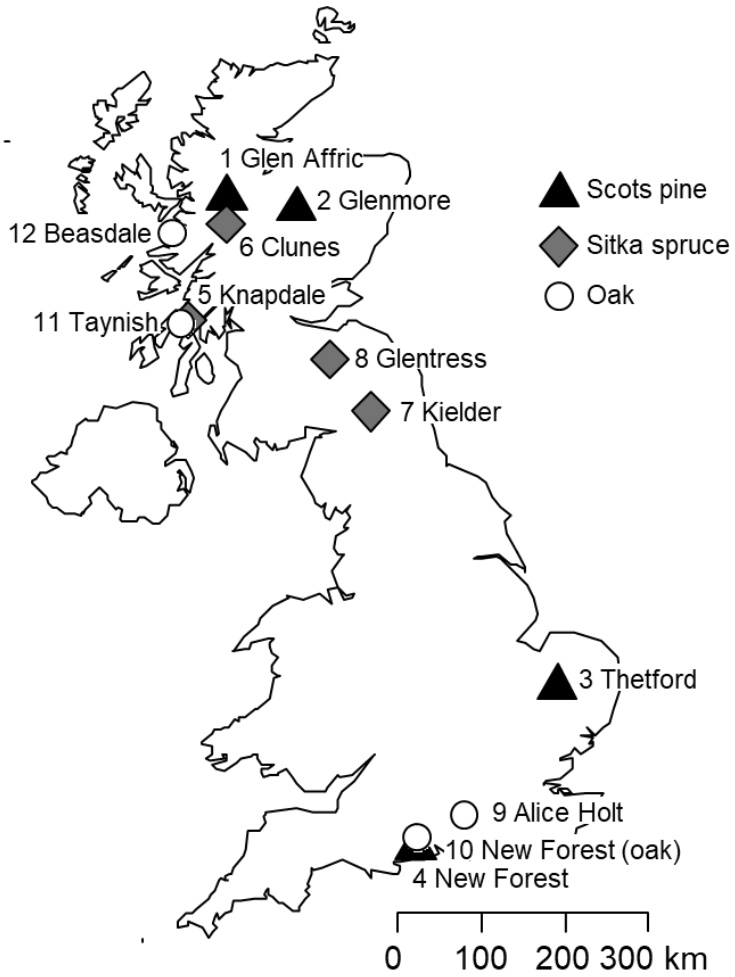


Figure 4.1: Locations of four Sitka spruce, Scots pine and Oak regional clusters across Great Britain. Each cluster of Sitka spruce and Scots pine is comprised of four stands, each representing four different stages of forest development and each oak cluster is comprised of two mature oak forest stands. Black triangles indicate the locations of Scots pine, grey diamonds the locations of Sitka spruce and white circles the location of oak.

Data collection

Spider sampling

Pitfall traps were used to collect ground-active spiders. Catches are biased towards more active and epigeal spider species, and so represent relative activity-density of these groups rather than absolute abundance of whole ground-dwelling communities (Thiele, 1977). Six traps were installed in a line running north to south through the centre of each study plot, with traps spaced at 10m intervals (Figure 4.2). Traps were 75mm in diameter, 110mm deep and contained 50ml of undiluted propylene glycol (antifreeze) as a temporary preservative. A 20cm x 20cm square cover made of galvanised steel was positioned three cm above the ground over the traps to prevent flooding of the traps, debris falling in and to minimise

access by small mammals. These lids each had 15cm-wide entrance holes at all four corners which were kept clear of leaf litter and any other debris. In areas known to have high densities of potentially disruptive mammals (New Forest and all Oak stands), traps were protected from trampling by a cage made from 250x250mm gauge mesh held in place by metal pegs. Neither lids nor mesh cages have been found to affect pitfall trapping efficiency (Siewers et al., 2014). During collections, samples from five traps were pooled and the sixth trap acted as a spare to be used if another trap was interfered with. The traps were run from the beginning of May for 20 consecutive weeks at each study plot in 2016 and 2017. Traps were reset every four weeks. Samples were pooled across the 20 weeks and two years in each plot. All adult spider species were identified using (Roberts, 1993). Nomenclature follows World Spider Catalog (2020). Information on species of conservation concern was taken from Harvey *et al.* (2017). This included species threatened with extinction based on IUCN Red List Categories as well as species with restricted distribution within Great Britain based on data from the National Spider Recording Scheme for England Scotland and Wales.

Quantifying Ground vegetation and litter structure of study plots

Each one ha study plot was split into four 50x50m quarters and each quarter was then split again in half diagonally. Vegetation quadrats measuring 2x2m were established in each diagonal half, resulting in eight quadrats per study plot (Figure 4.2). These were spaced at least 15m apart. Percentage cover to the nearest five percent was estimated for all vascular plant and moss species, as well as leaf and needle litter cover, during June and July 2017. Plot averages were estimated based on these eight quadrats. Keys to identify mosses and vascular plants included Atherton, Bosanquet and Lawley (2010) and Rose (1989, 2006), respectively. Needle and leaf litter depth was measured at four random points within a 10x10m sub-plot centred around each vegetation quadrat. The litter layer was measured from the forest floor surface to the fermentation layer (i.e. where litter was decomposing and no longer identifiable as needles or leaves).

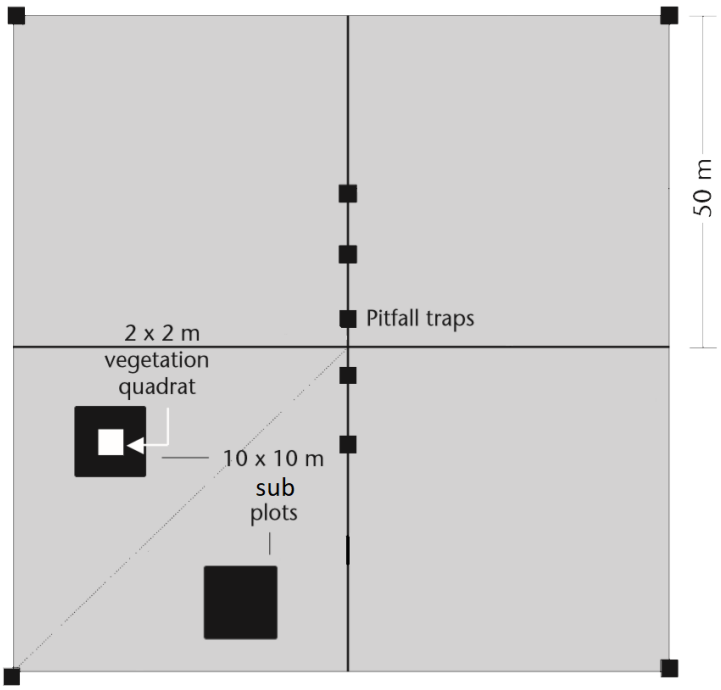


Figure 4.2: Study plot design amended from Humphrey, Ferris and Quine (2003)*. Vegetation quadrats and subplots were repeated within each quarter.*

Data analysis

Data preparation

To account for any differences in trapping effort between study plots, the abundance of each species in each plot was divided by the number of trap days in that plot and multiplied by the maximum number of trap days in all plots. Trap days per year ranged from 135 to 141, except at one site where, due to logistical reasons, traps were open for only 85 days during the first sampling season. Due to the unreliability of very rarely recorded species in contributing to patterns of occurrence across study plots, these species were removed from the data before analysis. A species was considered rare if it occurred twice or less throughout the study plots and sampling season, except where a species occurred once in each sampling season. This included 36 species accounting for 0.5% of all adult spiders caught. To explore differences between canopy tree species, all stands with a well-developed canopy were compared (mature and over-mature Scots pine and Sitka spruce and mature oak stands), giving eight replicates for each tree species.

Characterising ground vegetations structure and litter depth

In order to quantify the complexity of ground vegetation structure in study plots, vascular plant and moss species were classified by a combination of their average mature height and leaf distribution along the stem using species values derived from the LEDA plant trait database (Kleyer et al., 2008) and Grime, Hodgson and Hunt (1988). These traits were chosen since they would give an estimate of the number, location and diversity of potential anchor points for spider webs. The abundance-weighted diversity of plant structure was calculated using two common functional diversity indices: functional evenness (Feve) and Rao's quadratic entropy index (Rao). These each account for the number of unique growth forms, the similarity of growth forms and the cover of each growth form differently, with Feve giving more weight to the cover rather than identity or number of growth forms (Mason et al., 2005). High Feve would indicate different growth forms are equally common, whereas low Feve would indicate that a small number of growth forms dominate the community. The former would be considered more structurally diverse than the latter (Magurran, 1988). High Rao would also indicate a more structurally diverse plant community since it suggests growth forms are highly differentiated and cover is relatively evenly distributed between different growth forms (Mason et al., 2005). Rao and Feve were calculated using the "dbFD" function of the "FD" package (Laliberté et al., 2014; Laliberte and Legendre, 2010).

Generalised linear mixed models (GLMMs) were used to characterise changes in ground vegetation structure and diversity (Feve, Rao) and cover and leaf/needle litter depth across chronosequences of Scots pine and Sitka spruce and between canopy tree species. Stand stage or canopy tree species were included as a fixed factor and regional cluster (location) was included as a random factor for pine and spruce stand stage GLMMs only to account for the nested design. Gamma errors were used for Rao and Feve models since the response variable was bound between zero and one (Thomas et al., 2017). Gaussian errors were used to model vegetation cover and litter depth (Thomas et al., 2017). The "glmer" and "lmer" functions from the "lme4" package were used for gamma and gaussian errors

models, respectively (Bates et al., 2015). The significance of each model was tested using the “Anova” function of package “car” (Fox and Weisberg, 2011) with post hoc Tukey pairwise comparisons carried out to test for differences between stand stages or canopy tree species using the “glht” function of package “multcomp” (Hothorn et al., 2008). Holm corrections were used to correct p values for multiple comparisons (Holm, 1979). Where location was not found to explain any variation in a model, it was removed, and the model was re-run as a linear model (LM) for gaussian errors and a generalised linear model (GLM) for gamma errors using the “lm” and “glm” functions of the package “stats” (R Core Team, 2019).

Spider communities among stand stages and tree species

Spider species richness (SR) was compared across Scots pine and Sitka spruce stand stages and canopy tree species using sample-based rarefaction using the “iNEXT” function of package “iNEXT” (Chao et al., 2014; Hsieh et al., 2019). This method was used since it can correct for differences in sampling effort and abundance which is known to influence the number of species found (Chao and Chiu, 2016). Estimated richness was extrapolated to double the original abundance and significant differences were inferred where 95% confidence intervals did not overlap (Colwell et al., 2012).

Simpson’s index of species diversity (SD) was measured using the “diversity” function of the “vegan” package (Oksanen et al., 2019). This index was chosen because it is abundance-weighted and so is more influenced by common species than SR (de Bello et al., 2007; Simpson, 1949). SD and abundance were compared between stand stages and canopy tree species using GLMMs. Stand stage or canopy tree species and all ground vegetation and litter structure variables were included as fixed factors and location as a random factor. However, due to high correlation with vegetation cover, litter cover could not be included in models. Abundance was initially modelled using poisson errors due to zero-inflated count data (Zuur et al., 2009). However, overdispersion was detected for all abundance models and negative binomial errors were used instead (Thomas et al., 2017;

Zuur et al., 2009). SD was modelled using Gamma errors since this metric is bound between zero and one (Thomas et al., 2017). Model significance was tested using the “Anova” function and post-hoc Tukey pairwise comparisons with corrected p values were carried out to find differences between the levels of significant fixed factor variables using the “glht” function. As for environmental models, where location was not found to explain any variation in GLMMs, this variable was removed as a random factor and GLM were applied instead using the same error family. For GLMs, backward stepwise model refinement based on AIC scores was carried out to identify the best models using the “step” function of the “stats” package in R (R Core Team, 2019). Since this function does not work for mixed models, backward stepwise model refinement was carried out for GLMM manually by removing the least significant of the non-significant terms based on p values from the “drop1” function of the “stats” package until only significant terms remained (Thomas et al., 2017). At each step, both models were compared using the “anova” function of the “stats” package to test whether the variance explained by one model was significantly different to that of the other (Thomas et al., 2017).

The response of spider communities to stand variables was tested using multivariate regression tree analysis (MRT) using the “mvpart” function from the “mvpart” package (De’ath et al., 2013; Therneau and Atkinson, 2005). MRT is a form of constrained clustering which results in a tree of dichotomies (De’ath, 2002). Dichotomies are defined by a threshold value of explanatory variables, chosen to minimize dissimilarity within groups (Borcard et al., 2011). MRT was chosen because it is capable of analysing multivariate community data without making assumptions about the shape of the relationship between species and multiple explanatory variables and can handle interactions between explanatory variables (De’ath, 2002). In order to better understand the relative importance of tree species, stand age, ground vegetation structure and litter depth, spider assemblages from all forest types were included in this analysis. Spider community data was Hellinger transformed in order to reduce the influence of common species and this was converted to a Bray-curtis

dissimilarity matrix prior to analysis (Legendre and Gallagher, 2001). Bray-curtis dissimilarity was used because this does not treat shared absence of species as an indication of similarity between study plots (Legendre and Legendre, 2012). Explanatory variables included: latitude, longitude, tree species, stand age, percentage vegetation cover, Rao, Feve and litter depth. Since relationships between spider communities and stand development were not expected to be linear, stand stage was included as a categorical variable in previous models. However, since no assumptions are made about the shape of relationships in MRT, stand age could be included as a continuous variable. Litter cover was not included in the model since it was highly correlated with vegetation cover. The process was permuted 1000 times and the most frequently chosen size of tree (number of leaves or terminal nodes) based on lowest cross-validated relative error (CVRE) was chosen as the final tree. CVRE is considered to be a more conservative estimate of the predictive power of the tree and so is more commonly used to select tree size (De'ath, 2002). CVRE ranges from zero to one, with values closer to zero indicating better predictive power. It is possible for more than one variable to lead to the same split and the function will select a variable arbitrarily (Borcard et al., 2011). If this happened, all possible variables were reported. Significant indicator species for final groups were extracted using the "indval" function of the "labdsv" package (Dufrene and Legendre, 1997; Roberts, 2016).

All analyses were carried out in R (R Core Team, 2019).

Results

Overview

After removing infrequently occurring species, a total of 8012 adult spiders belonging to 97 species were identified across all study plots and both sampling years (3957 individuals from 88 species in pine, 2967 from 68 species in spruce and 1088 from 55 species in oak forests). 14 species of conservation concern with 105 occurrences across all study plots were identified (63 individuals from 12 species in pine, 37 individuals from 7 species in spruce and 5 individuals from 4 species in oak forests). Many of the species removed due to infrequent occurrences were also threatened species but could not be reliably included in analysis. See Appendix 4.2 for a list of species sampled, their conservation status and abundance across stand types.

Characterising ground vegetation structure and litter depth

Ground vegetation cover, Feve and Rao of ground vegetation, as well as litter depth were the same across all Scots pine stand stages. In contrast, in Sitka spruce vegetation cover, RAO and litter depth differed significantly across stand stages (χ^2 (3, N=16) = 31.63, p < 0.0001; χ^2 (3, N=16) = 14.12, p = 0.003; χ^2 (3, N=16) = 13.18, p = 0.004 respectively), being higher in pre-thicket and over-mature stands compared with mid-rotation and mature. Additionally, for both Rao and litter depth these metrics were lowest in mature stands and intermediate diversity in mid-rotation stands. Feve differed among Sitka spruce stand stages (χ^2 (3, N=16) = 7.65, p = 0.05), however, this significant difference was not upheld after correcting for multiple comparisons. Vegetation cover differed significantly among canopy tree species (χ^2 (2, N=24) = 4.23, p < 0.03). Scots pine stands had higher vegetation cover than Sitka spruce, whereas vegetation cover was intermediate in Oak stands. There were no significant differences between canopy tree species in terms of Feve, Rao or litter depth. Although litter cover was also measured, it was found to be highly inversely

correlated with vegetation cover and so was not included in any analysis (Figure 4.3, Appendix 4.3).

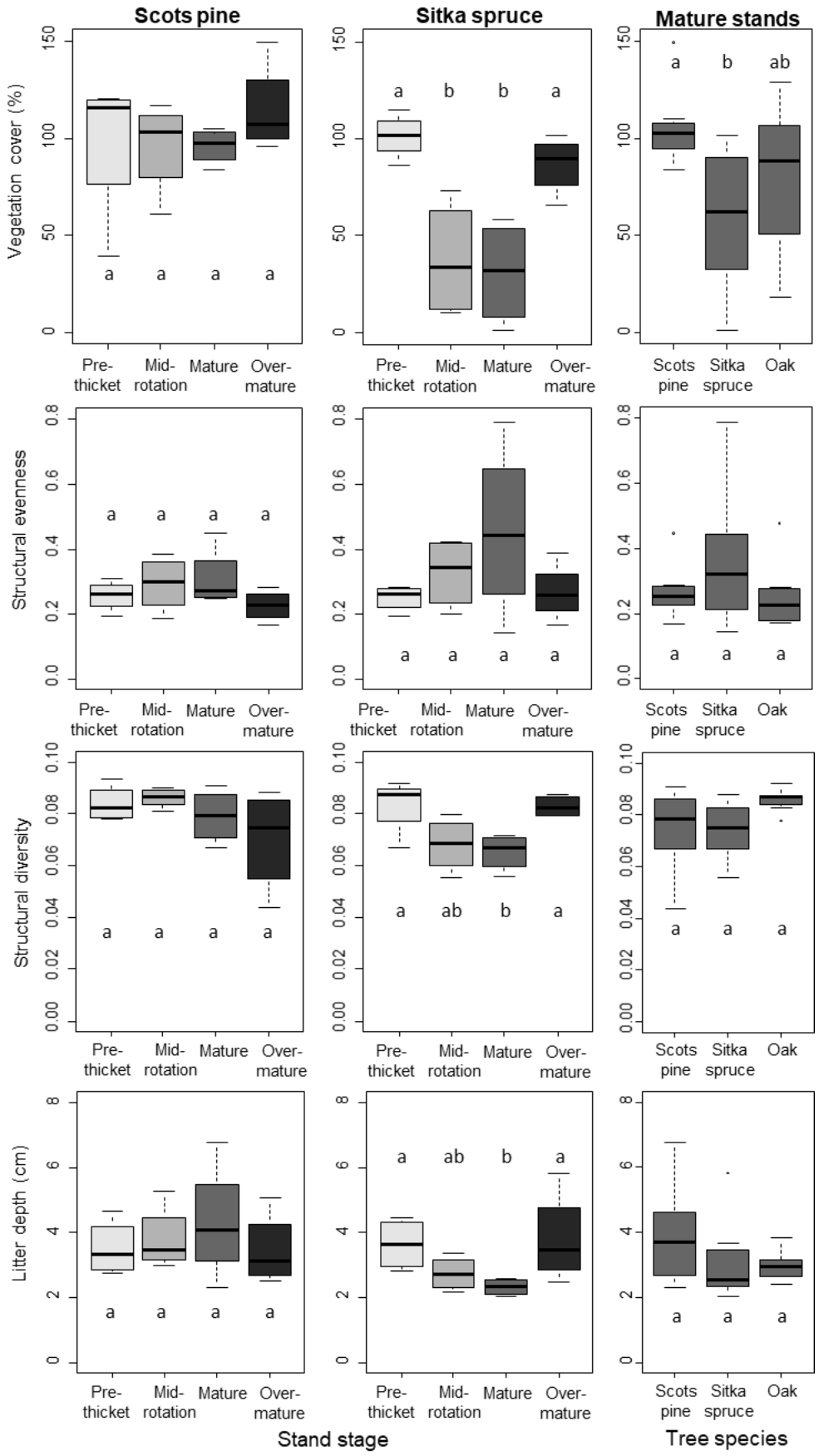


Figure 4.3: Ground vegetation and litter variables through Scots pine and Sitka spruce plantation forest stand stages and between mature stands of Scots pine, Sitka spruce and Oak. Letters indicate significance of post-hoc Tukey pairwise comparisons following GLMM analysis, with different letters indicating a significant difference.

Spider diversity and communities among stand stages and tree species

Spider SR was similar among the Scots pine stand stages (Figure 4.4, Appendix 4.3). However, in Sitka spruce, it was higher in pre-thicket stands compared to mid-rotation and mature stands, though not over-mature stands, which had intermediate richness. Across canopy tree species, SR in spruce was lower than that of pine and marginally lower than SR of oak stands, whereas oak and pine were similar to each other.

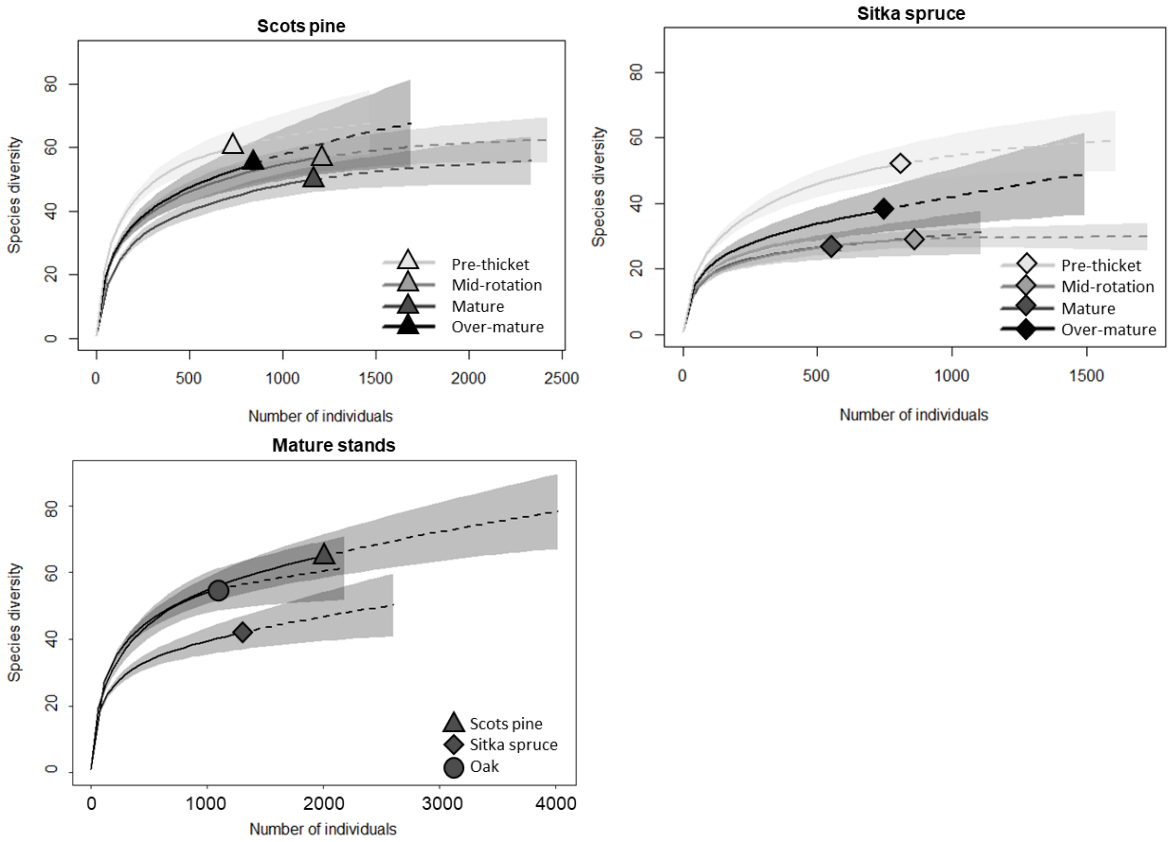


Figure 4.4: Rarefaction curves from sample-based rarefaction indicating spider species richness at different stand stages in Scots pine and Sitka spruce and for different canopy tree species (Scots pine, Sitka spruce and Oak). Grey bars indicate 95% confidence intervals and, where these do not overlap, stand stages are significantly different.

For spider abundance in pine stands, only stand stage and litter depth were retained in the final model, where stand stage had a near-significant effect (χ^2 (3, N=16) = 6.86, p = 0.08) and litter depth positively affected abundance (χ^2 (1, N=16) = 7.29, p = 0.006). In spruce, stand stage, Feve and litter depth were retained in the final model, however, none of these variables were found to affect abundance in these stands. In comparisons between canopy tree species, tree species and litter depth were retained in the final model of spider abundance. Abundance was higher in pine stands compared to oak and was intermediate

in Sitka spruce (χ^2 (2, *N*=24) = 10.42, *p* = 0.005). Litter depth had a positive effect on spider abundance (χ^2 (1, *N*=24) = 7.53, *p* = 0.006) (Figure 4.5, Appendix 4.3).

For Simpson's diversity in Scots pine and Sitka spruce stands, stand stage, Feve, Rao and litter depth were retained in the model, all of which significantly affected spider diversity. In pine stands, pre-thicket pine stands had the highest diversity but were not significantly more diverse than mid-rotation stands. Mature pine stands had lowest spider diversity, but only mid-rotation and pre-thicket stands were significantly more diverse than mature stands (χ^2 (3, *N*=16) = 27.49, *p* = $4.64e^{-6}$). Feve (χ^2 (1, *N*=16) = 14.48, *p* = 0.0001) and Rao (χ^2 (1, *N*=16) = 7.62, *p* = 0.006) of ground vegetation along with litter depth (χ^2 (1, *N*=16) = 12.23, *p* = 0.0005) had a positive effect on spider SD in pine stands. In Sitka spruce stands, spider diversity was highest in pre-thicket and over-mature stands, lowest in mature stands and intermediate in mid-rotation stands (χ^2 (3, *N*=16) = 30.29, *p* = $1.2e^{-6}$). As in pine stands, Feve (χ^2 (1, *N*=16) = 21.94, *p* = $2.83e^{-6}$), Rao (χ^2 (1, *N*=16) = 7.86, *p* = 0.005) and litter depth (χ^2 (1, *N*=16) = 8.31, *p* = 0.004) had a positive effect on spider SD. In models of different canopy tree species, only Feve was retained in the final model for spider diversity and this had a positive effect on diversity (χ^2 (1, *N*=24) = 4.19, *p* = 0.04) (Figure 4.5, Appendix 4.3).

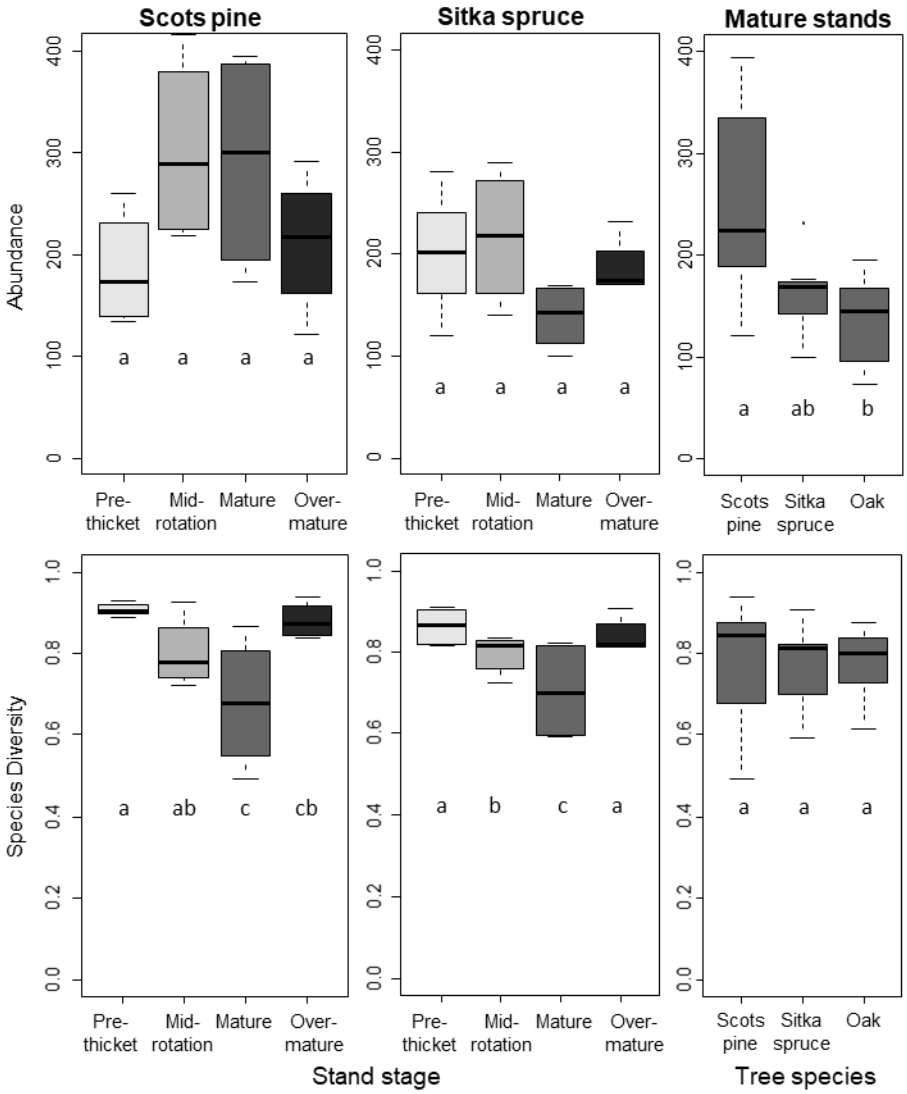


Figure 4.5: Boxplots comparing abundance and Simpson's index of species diversity across Scots pine and Sitka spruce stand stages and for different canopy tree species (Scots pine, Sitka spruce and Oak). Letters indicate significance of post-hoc Tukey pairwise comparisons with different letters indicating a significant difference.

Out of 1000 runs, the MRT analysis picked two and eight-leaf trees most frequently but the eight-leaf tree had low relative and cross-validated errors and was therefore selected for the final model (Figure 4.6). This model explained 77.1% of the variation in the data and the cross-validated error (0.57) suggests the model has moderate predictive power. The first split separated study plots by latitude but also could produce the same split by longitude, with plots in south-east England separated from those in north England and Scotland (49.07% of variance). The northern study plots were then further divided by stand age (8.52% of variance), resulting in a terminal node with stands under 11.5 years (group 5, n=4). The stands older than 11.5 years were then further split according to age (6.35% of

variance), with stands younger than 103.5 years separated from older stands. The oldest of these stands were split again according to vegetation cover (2.09% of variance), producing one terminal node where vegetation cover was less than 50.63% (group 3, n=2), and another where vegetation cover was higher (group 4, n=3). However, this split would have arisen if these sites were separated by either latitude or longitude. The final 19 northern study plots were split by litter depth (2.85% of variance), resulting in one terminal node with litter deeper than 2.69cm (group 1, n=11) and the other with shallower litter layers (group 2, n=8). The southern sites from the initial split were further divided according to litter depth (5.54% of variance), producing one terminal node where litter was deeper than 3.878 cm (group 8, n=4). The remaining study plots with lower leaf litter were split according to latitude (2.71% of variance), with northern plots forming one terminal node (group 6, n= 3) and the remaining southern plots, all from one region (New Forest) (group 7, n=5). Most terminal groups included a mixture of canopy tree species and stand stages except for group 4 (only Oak stands), group 5 (only pre-thicket), and group 8 (only Scots pine).

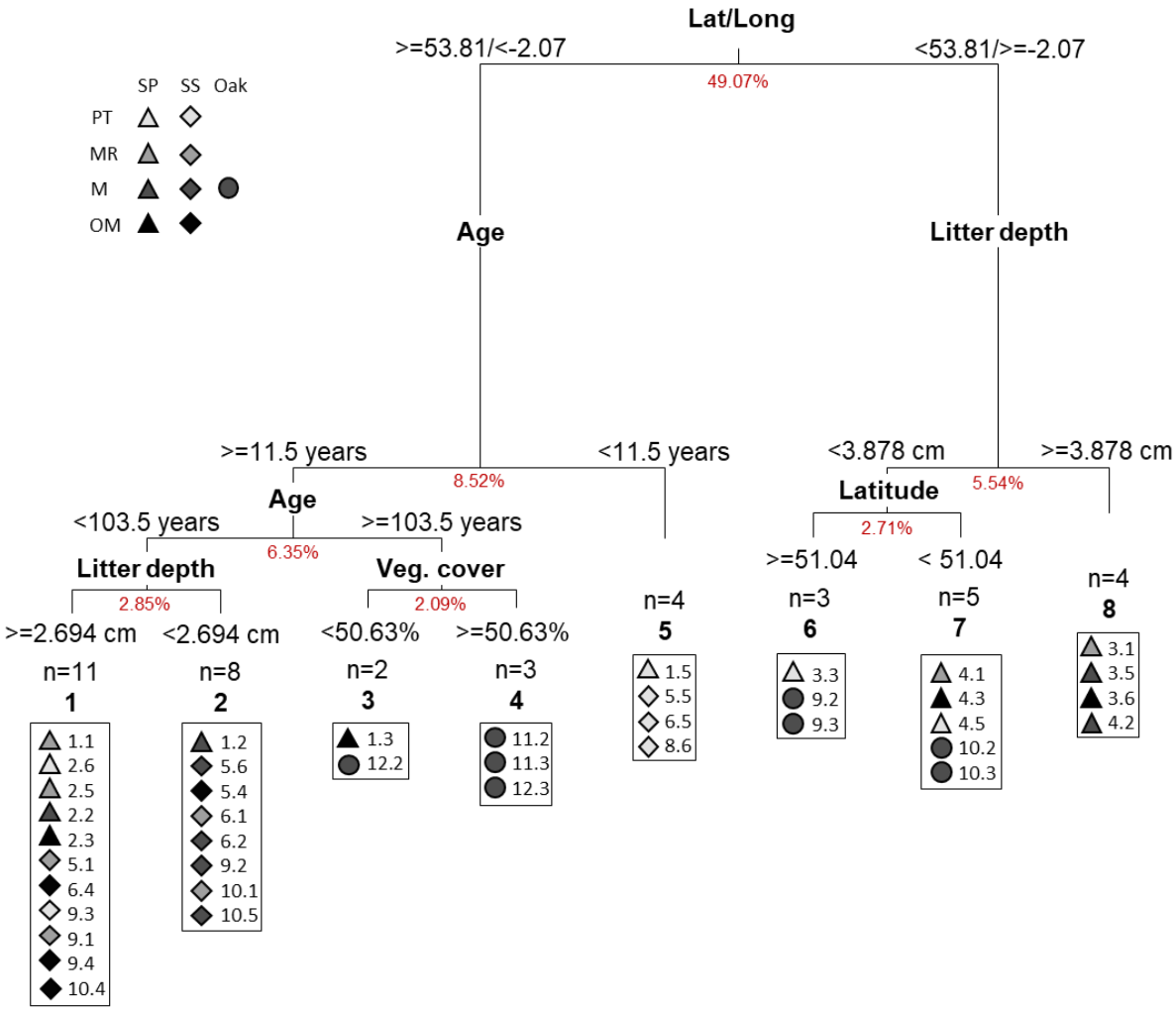


Figure 4.6: Multivariate regression tree (MRT) comparing Hellinger transformed abundance of spider species and seven stand variables using Bray-curtis similarity. 77.1% of variation in data was explained by this tree (cross-validated error 0.57). Variables driving splits indicated in bold text. Red text below nodes indicates variation explained by the corresponding node. Group number is shown in bold below each final leaf along with the number of study plots in each group and lists of study plots in each group. Triangles indicate Scots pine study plots, diamonds indicate Sitka spruce and circles indicate Oak. The lightest grey symbols indicate pre-thicket stand stages, light grey indicates mid-rotation, dark grey indicates mature and black symbols indicate over-mature. The split creating final leaves 3 and 4 could have resulted from differences in vegetation (shown), latitude (>= 51.04 left, < 51.04 right) and longitude (>= -1.19 left, < -1.19 right).

Indicator species analysis suggested 22 indicator species for the eight groups produced by the MRT (Table 4.2). There were three indicator species for groups 1 and 3, one indicator species for group 2, two indicator species for groups 4, 6 and 7, five indicator species for group 5 and four indicator species for group 8 (Table 4.2). Most indicator species were associated with forested habitats except for several of the species indicative of group 5 (pre-thicket Scots pine and Sitka spruce) which are associated with various open habitats. One species indicative of New Forest plots in group 7, *Scotina celans* is listed as nationally scarce.

Table 4.2: Indicator species for each multivariate regression tree final group including indicator value, p value and habitat associations. In group descriptions, SP represents Scots pine and SS represents Sitka spruce.

Group	Species	Family	Habitat association	Indicator value	P value
1 Northern 11.5-103.5 yrs Deep litter SP/SS	*Centromerus arcanus*	Linyphiidae	forest	0.44	0.026
	Porrhomma pallidum	Linyphiidae	forest	0.34	0.001
	Tapinocyba pallens	Linyphiidae	forest	0.37	0.004
2 Northern 11.5-103.5 yrs Shallow litter Mainly SP	*Monocephalus fuscipes*	Linyphiidae	forest	0.25	0.015
3 Northern >103.5 yrs Low veg cover SP/OAK	*Hahnia helveola*	Hahniidae	Forest/open	0.44	0.031
	Neon reticulatus	Salticidae	Forest/open	0.46	0.011
	Walckenaeria acuminata	Linyphiidae	Forest/open	0.20	0.045
4 Northern >103.5 yrs High veg cover OAK	*Tenuiphantes tenebricola*	Linyphiidae	Forest	0.37	0.017
	Tenuiphantes zimmermanni	Linyphiidae	Forest	0.19	0.023
5 Northern <11.5 yrs Mainly SS	*Agroeca proxima*	Linyphiidae	Open	0.42	0.042
	Drassodes cupreus	Gnaphosidae	Open	0.50	0.020
	Palliduphantes ericaeus	Linyphiidae	Open	0.27	0.001
	Micrargus herbigradus	Linyphiidae	Forest/open	0.22	0.040
	Walckenaeria vigilax	Linyphiidae	Humid	0.50	0.030
6 Southern Shallow litter Thetford/Alice holt SP/OAK	*Coelotes terrestris*	Agelenidae	Forest	0.48	0.023
	Robertus lividus	Linyphiidae	Forest/various	0.29	0.045
7 Southern Shallow litter New Forest SP/OAK	*Tenuiphantes flavipes*	Linyphiidae	Forest	0.49	0.004
	** Scotina celans*	Liocranidae	Forest/open	0.52	0.033
8 Southern Deep litter SP	*Agyneta conigera*	Linyphiidae	Forest	0.50	0.036
	Iberina montana	Hahniidae	Forest	0.44	0.031
	Pardosa saltans	Lycosidae	Forest	0.54	0.005
	Piratula hygrophila	Lycosidae	Forest/open	0.39	0.022

*Nationally scarce species

Species of conservation interest among stand stages and tree species

Twenty-seven nationally scarce, one nationally rare, one amber listed, two vulnerable, three endangered and one critically endangered spider species were sampled, including those excluded from analysis (Table 4.3). Nearly half (14 out of 35) of the listed species were found exclusively in Scots pine stands of various stages but pre-thicket pine stands supported more listed species than any of other stages. Three species were exclusive to Sitka spruce and six were exclusive to Oak stands. Mature Sitka spruce was the only canopy tree species x stand stage combination where no species of conservation concern were found.

Table 4.3: All species of conservation concern sampled, including status based on Harvey et al. (2017), stand type in which species were present, overall abundance and habitat associations based on the British Arachnological Society (BAS) Spider Recording Scheme (SRS) and Spiders of Europe. For statuses, NS indicates nationally scarce and NR nationally rare and both are unique categories to Great Britain. CE indicates critically endangered according to IUCN criteria, EN indicates endangered and VU indicates vulnerable. Amber indicates a species is between near threatened and least concern IUCN categories. For stand types, SP represents Scots pine, SS Sitka spruce, PT pre-thicket, MR mid-rotation, M mature and OM over-mature. An asterisk indicates that the species was not included in analysis.

		Stand type								
		Tree species			Stand stage					
Species	**Status**								**Abund.**	**Habitat association**
Centromerus incilium	NS	SP			PT				1	Grassland
Dipoena inornate	NS	SP			PT				1	Heath/grassland
Drassodes pubescens	NS	SP			PT				1	Heath/grassland
Euophrys herbigrada	VU	SP			PT				1	Grassland
Micaria subopaca	NS	SP			PT				1	Pine/oak trees
Scotina palliardii	EN	SP				MR			3	Grassland/Heath
Thyreosthenius biovatus	NS	SP				MR			1	With wood ants
Trachyzelotes pedestris	NS	SP				MR			1	Grassland
Pardosa lugubris	NS	SP					M		1	Pine forest
Xysticus luctator	EN	SP					M		3	Heath/Beech forest
Drassyllus praeficus	NS	SP						OM	1	Calcareous grassland
Zelotes petrensis	NR	SP						OM	1	Open
Zora nemoralis	VU	SP			PT			OM	2	Near forest
Scotina celans	NS	SP			PT	MR	M	OM	30	Forest edge
Allomengea scopigera	Amber		SS		PT				1	Wet open
Pityohyphantes phrygianus	NS		SS			MR			2	Shaded/Coniferous forest
Asthenargus paganus	NS		SS		PT	MR		OM	16	Forest
Centromerus albidus	CE			OAK			M		1	Beech forest
Centromerus levitarsis	EN			OAK			M		1	Damp forest/bog
Cicurina cicur	NS			OAK			M		1	Damp forest/shaded
Episinus maculipes	NS			OAK			M		1	Forest
Haplodrassus silvestris	NS			OAK			M		1	Forest
Walckenaeria obtuse	NS			OAK			M		1	Broadleaved forest
Agyneta cauta	NS	SP	SS		PT	MR			4	Forest edge/bog
Agyneta olivacea	NS	SP	SS		PT		M		4	Unknown
Saaristoa firma	NS	SP	SS		PT	MR		OM	6	Damp forest/heath
Maro minutus	NS	SP	SS		PT	MR	M	OM	16	Humid forest/bog
Porrhomma convexum	NS	SP	SS		PT	MR	M		11	Damp/shaded
Jacksonella falconeri	NS	SP		OAK			M		2	Heath
Walckenaeria furcillata	NS	SP		OAK	PT		M		3	Heath/forest
Walckenaeria dysderoides	NS	SP		OAK	PT	MR	M		8	Heath/forest
Walckenaeria incisa	NS	SP		OAK	PT		M	OM	3	Dry forest/various
Porrhomma campbelli	NS	SP	SS	OAK		MR	M	OM	5	Subterranean
Porrhomma montanum	NS	SP	SS	OAK	PT	MR	M	OM	25	Forest
Porrhomma oblatum	NS	SP	SS	OAK	PT	MR	M			Damp forest

Discussion

Spider communities among stand stages and tree species

We predicted that stand stage and tree species would be fundamental in shaping epigeal spider communities and that increased structural complexity (e.g. ground vegetation and leaf/needle litter) would lead to more diverse communities. We found that whilst structural parameters (e.g. litter depth, ground vegetation structural diversity and evenness) and stand age were important in shaping spider diversity and community composition, canopy tree species identity was less so. However, tree species, as well as litter depth, had an influence on spider abundance. Although tree species has been found to affect spider communities (Finch, 2005; Gallé et al., 2018), our results are generally supported by the literature which suggests that litter and ground vegetation are important drivers of epigeal spider diversity (Gallé et al., 2018, 2017; Isaia et al., 2015; Oxbrough et al., 2005; Sereda et al., 2012; Ziesche and Roth, 2008). In addition, some studies suggest that since these structural variables are not necessarily tied to stand type, stand type (stand age and canopy tree species) is less important than it may seem (Gallé et al., 2017; Ziesche and Roth, 2008).

We hypothesised that stands with higher ground vegetation cover, more structurally complex vegetation cover and deeper litter layers would support more diverse spider communities. This is supported in the Sitka spruce stands where pre-thicket and over-mature stands had more species rich and diverse spider communities than mid-rotation and mature stand stages. Further, higher structural diversity of vegetation and deeper litter in pre-thicket and over-mature spruce stands had a positive effect on spider diversity. It is worth noting that ground vegetation cover could not be included in the model of SD in spruce stands because it was highly correlated with stand stage, however, vegetation cover also declined during the middle stand stages of spruce forests. Stands with low vegetation cover and diversity and shallow litter were dominated by spiders from the Linyphiidae family such as *Tenuiphantes zimmermanni*, *Palliduphantes ericaeus, Monocephalus fuscipes* and

Centromerus arcanus, although only *M. fuscipes* was also less dominant in other stands. These spiders spin small, simple webs close to the ground and so are not thought to be as reliant on abundant or structurally complex vegetation as many other web-weaving spiders (Roberts, 1993). Indeed, they are often reported as being the dominant species in studies of epigeal spider communities in forests (Barsoum et al., 2014; Fuller et al., 2014; Oxbrough et al., 2010; Schuldt et al., 2008; Ziesche and Roth, 2008). It may be the case that this family of spiders is one of few with a strategy that allows it to survive in habitats with little ground vegetation and prey availability as well as those with more of these resources. Furthermore, Kumschick et al. (2009) found spiders of this family to be less energy-limited than other families, indicating that a lack of prey does not limit Linyphiid distribution.

Diverse vegetation structure and deep litter layers lead to opportunities for a wider range of hunting strategies and more complex webs as well as more abundant prey, a stable microclimate and shelter (Bultman and Uetz, 1982; Roberts, 1993; Russell, 1989; Uetz, 1991, 1979). Indeed, many other studies have found these variables to be important drivers of spider diversity in forests (Gallé et al., 2018; Isaia et al., 2015; Oxbrough et al., 2010). These results suggest that spider communities respond to a lack of food sources and opportunities for web-building in mid-rotation and mature spruce stands. In a similar study in the same forest type, spider diversity also declined as stands developed but began increasing again prior to commercial maturity as a result of thinning operations (Oxbrough et al., 2005). The spruce stands in this study were not thinned and so the natural dying of trees in over-mature stands is the first point at which the canopy begins to reopen. This is also when spider diversity increases. This suggests that management interventions which open the canopy, allowing ground vegetation to return, could prevent declines in spider diversity during the middle of the spruce forest harvest cycle. Indeed, Huang et al. (2014) have found that thinning interventions can alter spider communities in forests.

In pine stands the same variables as in spruce stands significantly explained variation in spider diversity (ground vegetation, litter depth and stand stage). This effect of stand stage

was unexpected since vegetation and litter structure did not change with stand development in this forest type. However, canopy cover was higher in mature pine stands compared to pre-thicket and this is thought to have a role in determining spider diversity and community composition (Gallé et al., 2018; Oxbrough et al., 2005). Unlike in spruce, spider SR and abundance were the same across all pine stand stages, with abundance only affected by litter depth. Litter depth influences prey availability, litter complexity (and therefore anchor points for webs) and microclimate (Uetz, 1979) and is, therefore, widely cited as being one of the most important factors for determining spider communities (Bultman and Uetz, 1982; Gallé et al., 2017; Isaia et al., 2015; Oxbrough et al., 2010; Schuldt et al., 2008). To our knowledge there are no studies of spiders among stand stages of Scots pine dominated forests, however, communities of ground-dwelling carabids have also been found to be less variable throughout Scots pine forest harvest cycles in comparison to those of Sitka spruce (Jukes et al., 2001).

Although we found that tree species *per se* was generally less important than other factors (e.g. vegetation cover, litter depth, stand age and location), we did find that spider communities in pine stands were more species rich than in spruce and more abundant than in oak. Pine plantations have been found to support more diverse spider communities than oak plantations (Barsoum et al., 2014), or Lodgepole pine plantations (Docherty and Leather, 1997). Though Lodgepole pine is not native and may be expected to have a lower number of associated species, this difference was attributed to differences in vegetation cover (Docherty and Leather, 1997). Further, where tree species has been identified in other studies as an important driver of spider community composition, this is usually due to its influence on other factors within the forest, such as those identified in this study (e.g. ground vegetation and leaf/needle litter depth) (Gallé et al., 2018, 2017; Ziesche and Roth, 2008). In our study, differences in vegetation cover between canopy tree species reflect differences in spider SR and so vegetation cover likely drives these differences in spider diversity. Vegetation cover is important for spiders since it affects microclimate and prey availability

and provides hunting opportunities and shelter (Bultman and Uetz, 1982; Roberts, 1993; Uetz, 1991). Overall, pine stands did not consistently support higher diversity than either oak or spruce stands, therefore, all three forest types have value in supporting spider communities.

Location was a more important factor than stand structure, tree species or age in explaining variation in spider community composition, with a predominantly north-south split in Northern England. Oxbrough et al. (2012) also found that location was more important than forest type, explaining variation in spider community composition in stands spread across ~350km. In contrast, Oxbrough et al. (2010) found that communities of closed canopy plantations across Ireland were highly similar, with no regional variation in stands separated by up to ~ 200km. However, in our study, stands are separated by up 750km and therefore it is perhaps unsurprising that this is important in driving community composition. North and south Great Britain have overlapping species pools but there are many species known to be restricted to each region, so this is expected to be an important factor, especially when sampling species at a national scale. (Roberts, 1993). Region was similarly found to have a large influence on spider diversity and community composition among forests across South England and Ireland (Barsoum et al., 2014) and this study suggests there is also a difference from north to south, as well as within southerly regions.

Whilst age was not the key driver, over the forest harvest cycle there was evidence of change in species from open-associated to forest associated. This is well documented for spiders (Oxbrough et al., 2005; Purchart et al., 2013) as well as other taxa (Butterfield, 1997; Koivula et al., 2002; Magura et al., 2015; Pawson et al., 2008) and is expected since young stands more closely resemble open habitats and support open habitat-associated species such as *Agroeca proxima* and *Drassodes cupreus* collected here. In older stand stages, there was some evidence of a reopening canopy, with indicator species typical of open habitats supported (e.g. *Neon reticulatus*, *Hahnia helveola* and *Walckenaeria*

acuminata). This phenomenon has been documented in other old forest stands with re-opening canopies (Oxbrough et al., 2010, 2005; Paradis and Work, 2011).

Species of conservation interest among stand stages and tree species

It is noteworthy that, collectively, the study plots representing common forest types were found to support a similar proportion (25%) of spider species of conservation concern as can be found amongst all spiders in Great Britain (20%) (Harvey et al., 2017). Further, stands of all developmental stages and tree species supported species of conservation concern, except for mature Sitka spruce stands. This supports the concept that all of the forests types surveyed here, which included intensively managed plantations, have a role to play in conservation (Brockerhoff et al., 2008; Quine and Humphrey, 2010). Nearly half of all listed species were found in Scots pine forests, with many of these sampled in pre-thicket pine only and associated with open habitats (e.g. *Centromerus incilium*, *Dipoena inornate*, *Drassodes pubescens*, *Euophrys herbigrada*, *Micaria subopaca*). In comparison, fewer listed spiders in terms of richness or abundance were found in Oak or Sitka spruce. The spruce stands had a smaller geographic spread than pine or oak and fewer listed species associated exclusively with this forest type may reflect regional variation. It could be expected that oak forests would support a greater proportion of species of conservation concern since they are less intensively managed than commercial plantations and are a native forest type in Great Britain (Brockerhoff et al., 2008). However, when considering only mature and over-mature stands of each tree species, oak forests supported fewer listed spiders than both Scots pine and Sitka spruce forests. Many of the spiders of conservation concern associated exclusively with pine forests are thought to prefer open habitats or forest edge, whereas those found in spruce and oak are generally associated with forest and otherwise shaded habitats. Pine forests may support higher numbers of listed species because this forest type has a relatively open canopy and so supports open habitat species as well as forest species.

Several of the sampled species of conservation concern are thought to be reliant on forest habitats. This includes one species which is restricted to spruce forests (*Pityohyphantes phrygianus*) and can dominate spider communities in the canopies of this forest type (Ashmole et al., 1978). *P. phrygianus* is thought to be nationally scarce, despite being associated with a widespread habitat, because it is a recent colonist of Great Britain (Ashmole et al., 1978; "Spider Recording Scheme," n.d.). Several other species associated with a range of forest types were found, including *Asthenargus paganus*, *Centromerus albidus*, *Cicurina cicur* and *Episinus maculipes* ("Spider Recording Scheme," n.d.). *Pardosa lugubris* is thought to be found only in ancient pine forests but was sampled from a commercially mature Scots pine stand in this study, suggesting that this species can inhabit plantation forests (Harvey et al., 2017; "Spider Recording Scheme," n.d.). Two forest-associated species threatened by conversion to coniferous plantations were exclusively sampled in mature oak woods (*Haplodrassus silvestris* and *Walckenaeria obtusa*) ("Spider Recording Scheme," n.d.). These results also indicate that some species of conservation concern are not able to survive in plantation forests and require more natural forest habitats.

Interestingly, several species said to be threatened by the afforestation of heath and grassland were exclusively sampled in closed forest stands in this study ("Spider Recording Scheme," n.d.). This included two endangered species (*Xysticus luctator* and *Scotina palliardii*). However, it is acknowledged that the general under-recording of spiders limits our understanding of their habitat requirements (Harvey et al., 2017; "Spider Recording Scheme," n.d.). On the other hand, pre-thicket stands were found to support listed species restricted to open habitats (*C. incilium*: grassland, *Di. Inornate*: heath/grassland*, Dr. pubescens*: heath/grassland*, E. herbigrada*: grassland*, Allomengea scopigera*: various wet open habitats) ("Spider Recording Scheme," n.d.), demonstrating the value of forested habitats prior to canopy closure, within plantations. Pre-thicket stands are present in the landscape in plantations managed by clearfelling and replanting, but not in those managed by continuous cover forestry, since this aims to maintain consistent canopy cover. Whilst it

is thought to benefit forest-associated species (Lindenmayer et al., 2012; Puettmann et al., 2015) this management may be detrimental to open habitat specialists which benefit from the more structurally diverse vegetation in young forest stands (Brockerhoff et al., 2008; Oxbrough et al., 2007).This may be particularly pertinent in landscapes of intensively managed agriculture, where initial planting enhances spider diversity following release from agricultural management such as intensive grazing (Oxbrough et al., 2006). Few studies have assessed or sampled rare species from plantation forests, however, young, open-canopy forest stands are regularly found to support diverse spider communities (Košulič et al., 2016; Oxbrough et al., 2010, 2005).

Many of the listed species were rare in the dataset, occurring only once or twice overall and so care must be taken when drawing conclusions from these results. However, three species were found at least 16 times during sampling. *Scotina celans* is associated with forest edge and was sampled from all stand stages of Scots pine a total of 30 times, but only from the New Forest. *A. paganus* was sampled 16 times from all stages of Sitka spruce except mature and is thought to be a forest generalist. *Maro minutus* was also sampled 16 times and was found in both pine and spruce and in all stand stages, but only in Scotland. These findings demonstrate that common forest types in Great Britain have an important role in supporting rare species of spider, including those associated with non-forested habitats.

Conclusions

Overall this study indicates tree species is less important than larger scale (region) or local scale (stand age, vegetation cover and litter depth) factors in driving community composition. Litter depth was indicated as an important variable in determining spider diversity, abundance and community composition. Overall, we found distinct groups of spider communities with several forest-associated spiders depending on these factors. This suggests that forests in Great Britain, including semi-natural native forests, planted native forests and planted non-native forests of all stand stages provide a range of different forest

habitats, supporting unique spider communities and species of conservation interest and therefore have conservation value. Although pre-thicket stands were not as valuable in supporting forest-associated spider species, they did support open habitat species, including species of conservation value. Therefore, the value of this stand stage for the conservation of spiders should not be overlooked, especially in heavily degraded landscapes dominated by agriculture.

The oak stands were not intensively managed and are considered semi-natural, so it is surprising that they do not support more diverse spider communities than both conifer plantation types (Brockerhoff et al., 2008). It is possible that Great Britain does not have forest specialist communities due to the long history of low forest cover (5% forest cover 100 years ago and 15% 1000 years ago (Forest Research, 2019)). It has been demonstrated that many forest specialists are restricted to interior forest, at least a kilometre from forest edge (Ewers and Didham, 2008) and such species are likely to have been lost along with forest cover in Great Britain. Therefore, it is unclear if the lack of differences by forest type is due to forest type not being important or the absence of a specialist community in Great Britain. Although mature spruce stands did not support diverse communities of spiders and did not support any species of conservation concern, the importance of stand structure rather than stand type in determining spider communities suggests that it is possible to manage these stands in a way that contributes better to the conservation of spiders. In particular, in Great Britain where forest cover is very low, plantation forests can play an important role in supporting what remains of native forest communities (Bremer and Farley, 2010; O'Callaghan et al., 2017; Pawson et al., 2008; Quine and Humphrey, 2010).

Chapter 4 Appendices

Appendix 4.1: Locations and characteristics of pre-thicket (PT), mid-rotation (MR), mature (M) and over-mature (OM) Scots pine, Sitka spruce ad oak study plots.

Location	Study plot number	Stand stage	Age at sampling	% of main tree species	Rotation	Previous land use	Study plot locations		Plot elevation (m.a.s.l.)
							Lat	long	
Scot's pine									
Glen	1.5	PT	4	100	2	Native pinewood	57.261	-4.878	240
Affric	1.1	MR	32	94	1	Heath/grassland	57.347	-4.721	200
	1.2	M	55	95	1	Heath/grassland	57.293	-4.858	300
	1.3	OM	116	95	1	Native pinewood	57.27	-4.866	190
Glenmore	2.6	PT	11	70	2+	Native pinewood	57.153	-3.704	400
	2.5	MR	28	70	1	Native pinewood	57.152	-3.706	400
	2.2	M	52	81	1	Native pinewood	57.194	-3.751	380
	2.3	OM	84	90	1	Native pinewood	57.17	-3.674	430
Thetford	3.3	PT	8	63	2	Heath/grassland	52.4293	0.6849	60
	3.1	MR	38	100	1	Heath/grassland	52.4749	0.7006	30
	3.5	M	75	80	1	Heath/grassland	52.4702	0.716	50
	3.6	OM	109	100	1	Heath/grassland	52.4252	0.6335	20
New Forest	4.5	PT	21	100	2+	Native oakwood	50.8449	-1.6847	50
	4.1	MR	46	88	1	Native oakwood	50.8564	-1.6403	30
	4.2	M	69	80	1	Native oakwood	50.8453	-1.5281	20
	4.3	OM	86	68		Native oakwood	50.8327	-1.5173	30
Sitka spruce									
Knapdale	5.5	PT	9	100	2+	Heath/scrub	56.0822	-5.3289	150
	5.1	MR	29	100	2	Heath/scrub	56.0596	-5.5136	160
	5.6	M	44	86	2+	Heath/scrub	56.0635	-5.5087	100
	5.4	OM	82	82	1	Heath/scrub	56.0624	-5.5099	130
Clunes	6.5	PT	10	100	2+	Heath	56.9971	-4.888	180
	6.1	MR	28	92	2	Heath	57.003	-4.8706	80
	6.2	M	48	95	1	Heath/native woodland	56.9737	-4.9888	330
	6.4	OM	87	100	1	Heath	57.0002	-4.8839	140
Kielder	7.3	PT	16	100	2	Grassland	55.1565	-2.5183	320
	7.1	MR	26	78	2	Grassland	55.1679	-2.4492	260
	7.2	M	43	100	2	Grassland	55.1472	-2.4593	280
	7.4	OM	89	98	1	Grassland/mire	55.1406	-2.466	310
Glentress	8.6	PT	7	80	2+	Heath/grassland	55.6707	-3.1466	460
	8.1	MR	30	100	2	Heath/grassland	55.6662	-3.1517	380
	8.5	M	49	100	1	Heath/grassland	55.6651	-3.1556	310
	8.4	OM	81	100	1	Grassland	55.6203	-3.1051	290
Oak									
Alice Holt	9.2	MR	82	n/a	n/a	Native woodland	51.154	-0.865	90
	9.3	M	197	n/a	n/a	Native woodland	51.162	-0.852	70
New	10.2	MR	81	n/a	n/a	Native woodland	50.931	-1.639	70
Forest	10.3	M	188	n/a	n/a	Native woodland	50.838	-1.615	20
Taynish	11.2	MR	121	n/a	n/a	Native oakwood	56.003	-5.639	40
	11.3	M	129	n/a	n/a	Native oakwood	56.008	-5.592	50
Beasdale	12.2	MR	128	n/a	n/a	Native oakwood	56.897	-5.767	80
	12.3	M	149	n/a	n/a	Native oakwood	56.791	-5.76	30

Appendix 4.2: Species list and abundances

Table a) Spider conservation status and summed abundance across both sampling periods. PT represents pre-thicket stands, MR mid-rotation, M mature and OM over-mature. Infrequent species removed from data prior to analysis indicated by an Asterix. Conservation statuses represent the following: (LC – least concern, NS – nationally scarce, VU - vulnerable, EN - endangered, CR(PE) – critically endangered (possibly extinct))

Species	Conservation status	Scots pine				Sitka spruce				Oak
		PT	MR	M	OM	PT	MR	M	OM	M
Agroeca brunnea	LC	1	1	2	1	0	0	0	0	10
Agroeca proxima	LC	4	0	0	0	1	0	0	0	0
Agyneta cauta	NS	0	2	0	0	2	0	0	0	0
Agyneta conigera	LC	0	0	2	1	0	0	0	0	0
Agyneta olivacea	NS	1	0	2	0	1	0	0	0	0
Agyneta ramosa	LC	7	21	3	5	34	5	0	0	15
Agyneta subtilis	LC	2	4	10	3	1	0	0	0	3
*Allomengea scopigera**	Amber	0	0	0	0	1	0	0	0	0
Alopecosa pulverulenta	LC	1	1	0	1	5	0	0	0	0
*Amaurobius fenestralis**	LC	0	0	2	0	0	0	0	0	0
*Amaurobius ferox**	LC	0	0	1	0	0	0	0	0	0
Asthenargus paganus	NS	0	0	0	0	1	9	0	6	0
*Bathyphantes approximatus**	LC	0	0	0	0	1	0	0	0	0
Bathyphantes gracilis	LC	1	0	0	1	5	3	0	1	1
Bathyphantes parvulus	LC	4	0	0	0	1	2	0	1	2
*Centromerus albidus**	CR(PE)	0	0	0	0	0	0	0	0	1
Centromerus arcanus	LC	39	51	0	9	82	136	10	39	0
Centromerus dilutus	LC	12	14	12	19	5	25	11	19	3
*Centromerus incilium**	NS	1	0	0	0	0	0	0	0	0
*Centromerus levitarsis**	EN	0	0	0	0	0	0	0	0	1
Centromerus prudens	LC	0	0	0	0	1	0	2	0	0
Centromerus sylvaticus	LC	4	7	7	4	16	3	0	7	5
Ceratinella brevipes	LC	0	1	1	4	11	0	0	0	0
*Cicurina cicur**	NS	0	0	0	0	0	0	0	0	1
Clubiona reclusa	LC	1	0	0	0	0	0	0	1	0
Clubiona terrestris	LC	0	2	0	3	0	0	0	0	5
Cnephalocotes obscurus	LC	0	0	0	0	3	0	0	0	0
Coelotes atropos	LC	0	0	0	0	2	0	0	0	1
Coelotes terrestris	LC	0	16	0	0	0	0	0	0	75
Cryphoeca silvicola	LC	10	6	39	5	3	1	6	3	0
Dicymbium tibiale	LC	4	0	0	0	2	0	0	0	2
*Dipoena inornata**	NS	1	0	0	0	0	0	0	0	0
Diplocephalus latifrons	LC	0	1	0	0	0	1	16	5	5
*Diplocephalus picinus**	LC	0	0	0	0	0	0	0	0	2
Diplostyla concolor	LC	0	11	0	0	0	0	0	0	21
Dismodicus bifrons	LC	3	0	1	0	0	0	0	0	0
Drassodes cupreus	LC	1	0	0	0	5	0	0	0	0
*Drassodes pubescens**	NS	1	0	0	0	0	0	0	0	0
Drassyllus praeficus	NS	0	0	0	1	0	0	0	0	0
*Drassyllus pusillus**	LC	0	0	0	1	0	0	0	0	0
Dysdera crocata	LC	0	0	0	0	0	0	0	0	1
Dysdera erythrina	LC	0	0	0	0	0	0	0	0	1
*Episinus maculipes**	NS	0	0	0	0	0	0	0	0	1
*Erigonella hiemalis**	LC	0	0	0	0	1	0	0	0	0
*Ero cambridgei**	LC	0	0	0	0	0	0	0	0	2
Euophrys frontalis	LC	0	0	3	0	0	0	0	0	0
*Euophrys herbigrada**	VU	1	0	0	0	0	0	0	0	0
Gonatium rubellum	LC	0	4	1	9	0	0	0	0	1
*Gonatium rubens**	LC	1	0	0	0	0	0	0	0	0
Gongylidiellum vivum	LC	6	0	0	0	0	0	0	6	2
Hahnia helveola	LC	3	3	14	8	0	0	0	0	3
Haplodrassus signifer	LC	0	2	0	0	2	0	0	0	2
*Haplodrassus silvestris**	NS	0	0	0	0	0	0	0	0	1
Hilaira excisa	LC	3	107	0	2	0	0	1	4	0
Iberina montana	LC	0	7	11	2	0	0	0	1	0
*Jacksonella falconeri**	NS	0	0	1	0	0	0	0	0	1
*Lathys humilis**	LC	0	0	0	1	0	0	0	0	0
*Linyphia hortensis**	LC	0	0	0	0	0	0	1	0	1
Macrargus rufus	LC	0	4	10	0	0	0	2	3	4
Maro minutus	NS	5	2	0	0	0	0	8	1	0
Metellina mengei	LC	0	0	1	1	0	0	0	1	0

Species	Conservation status	Scots pine				Sitka spruce				Oak
		PT	MR	M			PT	MR	M	
Metellina merianae	LC	0	0	0	0	0	0	1	1	1
*Metellina segmentata**	LC	0	1	0	0	0	0	0	0	0
Micaria pulicaria	LC	3	0	0	0	2	0	0	0	1
*Micaria subopaca**	NS	1	0	0	0	0	0	0	0	0
Micrargus apertus	LC	13	10	4	11	16	15	4	3	7
Micrargus herbigradus	LC	33	44	17	30	53	36	18	27	16
Microneta viaria	LC	0	4	7	14	0	0	0	0	45
Minyriolus pusillus	LC	4	0	0	3	1	0	0	0	0
Monocephalus fuscipes	LC	18	41	25	13	23	69	40	51	37
Neon reticulatus	LC	11	7	6	7	2	0	0	0	5
*Neriene clathrata**	LC	0	0	0	2	0	0	0	0	0
Neriene montana	LC	0	0	0	1	0	0	0	0	2
Neriene peltata	LC	0	1	0	0	1	0	0	1	0
Obscuriphantes obscurus	LC	0	0	0	1	1	0	0	0	0
*Oedothorax gibbosus**	LC	0	0	1	0	0	0	0	0	0
Ozyptila trux	LC	1	9	1	2	0	0	0	0	15
Pachygnatha degeeri	LC	0	0	1	0	0	0	0	0	3
Pachygnatha listeri	LC	0	0	3	1	0	0	0	0	4
Palliduphantes ericaeus	LC	107	23	16	73	125	49	12	80	20
Palliduphantes pallidus	LC	7	7	6	29	5	20	8	18	44
*Pardosa lugubris**	NS	0	0	1	0	0	0	0	0	0
Pardosa pullata	LC	43	1	0	0	35	0	0	0	3
Pardosa saltans	LC	5	110	141	149	0	0	0	0	39
Pelecopsis mengei	LC	0	0	0	0	3	0	0	0	0
Phrurolithus festivus	LC	4	0	1	0	0	0	0	0	0
*Pirata piraticus**	LC	1	0	0	0	0	0	0	0	0
Piratula hygrophila	LC	64	264	493	85	37	0	0	3	132
Piratula uliginosa	LC	7	0	1	10	8	0	0	2	0
Pityohyphantes phrygianus	NS	0	0	0	0	0	2	0	0	0
*Pocadicnemis juncea**	LC	1	0	0	0	0	0	0	0	0
Pocadicnemis pumila	LC	4	2	2	1	3	0	0	0	2
Porrhomma campbelli	NS	0	0	0	1	0	2	1	0	1
Porrhomma convexum	NS	0	1	0	0	3	1	6	0	0
Porrhomma montanum	NS	3	5	2	0	1	1	8	4	1
Porrhomma oblitum	NS	2	0	0	0	0	3	0	0	2
Porrhomma pallidum	LC	5	25	11	8	12	33	17	13	3
Porrhomma pygmaeum	LC	0	2	1	2	1	0	2	1	1
Robertus lividus	LC	37	23	17	5	53	7	0	10	40
Saaristoa abnormis	LC	32	52	20	38	75	16	19	26	41
Saaristoa firma	NS	0	1	0	1	1	2	0	1	0
Scotina celans	NS	14	1	2	5	0	0	0	0	0
Scotina palliardii	EN	0	3	0	0	0	0	0	0	0
Silometopus elegans	LC	0	0	0	0	3	0	0	0	0
Tapinocyba pallens	LC	13	29	22	16	6	79	11	24	0
*Tapinopa longidens**	LC	0	0	0	0	0	1	0	0	0
Tenuiphantes alacris	LC	5	31	2	40	4	10	4	28	4
*Tenuiphantes cristatus**	LC	0	0	0	0	1	0	0	0	0
Tenuiphantes flavipes	LC	1	50	15	21	0	2	8	1	17
Tenuiphantes mengei	LC	6	2	0	1	7	0	0	0	0
Tenuiphantes tenebricola	LC	1	2	6	3	0	21	65	60	35
Tenuiphantes tenuis	LC	2	0	0	1	0	2	1	0	1
Tenuiphantes zimmermanni	LC	55	95	162	118	77	271	267	246	360
Theonoe minutissima	LC	3	2	0	0	0	0	0	1	0
*Thyreosthenius biovatus**	NS	0	1	0	0	0	0	0	0	0
Tiso vagans	LC	3	0	0	0	0	0	0	0	0
*Trachyzelotes pedestris**	NS	0	1	0	0	0	0	0	0	0
Trochosa terricola	LC	23	16	13	8	20	0	0	0	4
Walckenaeria acuminata	LC	14	18	18	10	24	20	11	27	30
*Walckenaeria antica**	LC	0	0	0	0	2	0	0	0	0
Walckenaeria atrotibialis	LC	15	3	2	6	2	0	0	0	3
Walckenaeria cucullata	LC	21	45	10	36	1	0	0	0	3
Walckenaeria cuspidata	LC	3	0	0	0	0	0	0	0	2
Walckenaeria dysderoides	NS	2	4	1	0	0	0	0	0	1
Walckenaeria furcillata	NS	1	0	0	0	0	0	0	0	2
Walckenaeria incisa	NS	1	0	0	1	0	0	0	0	1
Walckenaeria nudipalpis	LC	10	12	14	13	14	21	1	19	1
*Walckenaeria obtusa**	NS	0	0	0	0	0	0	0	0	1
Walckenaeria vigilax	LC	2	0	0	0	2	0	0	0	0
*Xysticus erraticus**	LC	0	0	0	0	1	0	0	0	0

Species	Conservation status	Scots pine				Sitka spruce				Oak
		PT	MR	M	OM	PT	MR	M	OM	M
Xysticus luctator	EN	0	0	3	0	0	0	0	0	0
Zelotes apricorum	LC	0	1	1	0	0	0	0	0	0
*Zelotes petrensis**	NR	0	0	0	1	0	0	0	0	0
Zora nemoralis	VU	1	0	0	1	0	0	0	0	0
Zora spinimana	LC	3	0	2	0	0	0	0	0	0
Zygiella x-notata	LC	0	1	0	0	0	0	0	6	0

Appendix 4.3: Summary statistics from models

Table a) vegetation structure and leaf/needle litter variables modelled against stand stage. Darker grey shading indicates significant effects (p < 0.05) and lighter grey shading indicates near-significant effects (p < 0.1).

Tree species	Response Variable	Error family	Mixed model?	Model term significance			Pair-wise comparisons (where overall model is significant or near-significant)					
				χ^2	df	*p*	PT-MR	PT-M	PT-OM	MR-M	MR-OM	M-OM
Pine	Veg cover	Gaussian	n	0.48	3	0.70						
	Feve	Gamma	y	4.81	3	0.19						
	Rao	Gamma	y	6.27	3	0.10	0.97	0.97	0.21	0.93	0.11	0.70
	Litter depth	Gaussian	y	1.41	3	0.70						
Spruce	Veg cover	Gaussian	y	31.63	3	**6.26e^{-7}**	**1.53e^{-4}**	**2.56e^{-5}**	0.68	0.68	**0.004**	**0.001**
	Feve	Gamma	y	7.65	3	**0.05**	0.84	0.14	0.84	0.75	0.84	0.20
	Rao	Gamma	n	14.12	3	**0.003**	0.07	**0.02**	1	1	0.07	**0.02**
	Litter depth	Gaussian	y	13.18	3	**0.004**	0.19	**0.03**	0.77	0.77	0.11	**0.01**

Table b) vegetation structure and leaf/needle litter variables modelled against canopy tree species. Darker grey shading indicates significant effects (p < 0.05) and lighter grey shading indicates near-significant effects (p < 0.1).

Response variable	Error family	Model term significance			Pair-wise comparisons (where overall model is significant or near-significant)		
		χ^2	df	*p*	SP-OAK	SS-OAK	SS-SP
Vegetation cover	Gaussian	4.23	2	**0.03**	0.27	0.41	**0.02**
Feve	Gamma	3.07	2	0.22			
Rao	Gamma	4.89	2	0.09	0.14	0.12	1.00
Litter depth	Gaussian	1.57	2	0.23			

Table c) Spider abundance and diversity modelled against stand stage, ground vegetation variables and litter depth. Darker grey shading indicates significant effects ($p < 0.05$) and lighter grey shading indicates near-significant effects ($p < 0.1$).

Tree species	Response variable	Error family	Mixed model?	Stand stage significance			Pair-wise comparisons (where overall model is significant or near-significant)					
				χ^2	df	*p*	PT-MR	PT-M	PT-OM	MR-M	MR-OM	M-OM
Pine	Abundance	negative binomial	n	7.79	3	**0.05**	0.09	0.14	0.92	1.00	0.32	0.42
	Diversity	Gamma	y	17.67	3	**5.14e^{-4}**	0.27	**5.23e^{-4}**	0.68	0.09	0.39	**0.002**
Spruce	Abundance	negative binomial	n	7.59	3	0.06	1	0.14	1	**0.05**	1	0.31
	Diversity	Gamma	y	13.25	3	**0.004**	0.49	**0.004**	0.71	0.16	0.71	**0.01**

Tree species	Response variable	Error family	Mixed model?	Vegetation cover				Feve				Rao				Litter depth			
				est	χ^2	df	*p*	est	χ^2	df	*p*	est	χ^2	df	*p*	est	χ^2	df	*p*
Pine	Abundance	negative binomial	n													0.15	7.29	1	**0.007**
	Diversity	Gamma	y					1.65	14.48	1	**0.0001**	9.09	7.62	1	**0.006**	0.09	12.23	1	**0.0005**
Spruce	Abundance	negative binomial	n					-0.60	2.09	1	0.15					0.10	2.29	1	0.13
	Diversity	Gamma	y					0.70	21.94	1	**2.82e^{-6}**	5.93	7.86	1	**0.005**	0.09	8.31	1	**0.004**

Table d) Spider Simpsons index of species diversity modelled against canopy tree species, ground vegetation and litter depth. Darker grey shading indicates significant effects (p < 0.05) and lighter grey shading indicates near-significant effects (p < 0.1).

Response variable	Error family	Canopy tree species significance			Pair-wise comparisons (where overall model is significant or near-significant)		
		χ^2	df	*p*	SP-OAK	SS-OAK	SS-SP
Abundance	Negative binomial	10.42	2	**0.005**	**0.004**	0.26	0.06
Diversity	Gamma						

Response variable	Error family	Vegetation cover				Feve				Rao				Litter depth			
		est	χ^2	df	*p*	est	χ^2	df	*p*	est	χ^2	df	*p*	est	χ^2	df	*p*
Abundance	negative binomial													0.14	7.53	1	**0.006**
Diversity	Gamma					0.58	4.19	1	**0.04**								

Chapter 5

Conclusions

This research investigated the taxonomic and functional diversity of forests of three of the most common tree species in Great Britain. This is the first multi-taxa, long-term, landscape scale study of forests in Great Britain including all major developmental stages of the clearfell forest harvest cycle, as well as the largest scale study of Scots pine forests in Great Britain. We aimed to explore the effect of environmental filtering through clearfell forest harvest cycles, as well as long-term changes in these forests. An additional novelty of this work is the joint approach of functional and taxonomic analyses to gain further insight into the mechanisms driving change in these ecosystems. This study also comprises the largest study of spiders within forests in Great Britain in terms of the forest types studied and the geographical range covered. This research delivers an evidence base for forest management guidelines provided by the UK Forestry Standard, including the provisioning of a range of stand structures and semi-natural and ancient forest within plantation forest landscapes.

The value of joint functional and taxonomic approaches

Traditionally, taxonomic metrics have been used to assess biodiversity and assumptions have been made about how biodiversity relates to the health and function of ecosystems. However, this is no longer thought to be appropriate. Instead, comparisons of taxonomic and functional metrics can be useful in revealing underlying mechanisms and deepening our understanding (Cadotte et al., 2011; De Bello et al., 2010). Overall, functional and taxonomic metrics were broadly similar over the 20-year study period (Chapter 3) and showed similar changes over the forest harvest cycle though effects were often subtle (Chapter 2). For example, trends in functional and taxonomic diversity were similar for each taxonomic group across Sitka spruce forest harvest cycles, although these were never both

significant within the same taxon (Chapter 2). On the other hand, neither functional nor taxonomic diversity changed through the Scots pine forest harvest cycle for any taxonomic group (Chapter 2). Similarly, almost universally negative trends in diversity were found over the 20-year study period, but these trends were more notable for taxonomic diversity than for functional diversity (Chapter 3). Although these differences between functional and taxonomic responses were subtle, they can indicate underlying mechanisms or outcomes of changes in these communities. For example, where there is a stronger effect on functional diversity, this can indicate changes in ecosystem function despite no observed effect on taxonomic diversity (De Bello et al., 2010). On the other hand, a stronger effect on taxonomic diversity can indicate a loss of functional redundancy which will result in vulnerability to stochastic events (Cadotte et al., 2011). These are both important processes and this study highlights the value of the functional trait approach in assessing ecosystem impacts. However, very careful consideration of functional trait selection is required, and this is something that needs further development, particularly for less well studied taxa such as carabids, spiders and mosses. A better range of relevant traits to select from would increase the scope of studies, especially for arthropods, many groups of which have no trait information available. In particular, very little is known about the functional effects of arthropods and this restricts how they can be studied. For example, functional redundancy can tell us about the resilience of ecosystem functions but, since it requires effect traits, this cannot be measured for many taxa (Rosenfeld, 2002). In addition, development of our understanding of the relationship between traits and the environment or ecosystem services would improve confidence in our interpretation and application of results.

The value of multi-taxa approaches

The multi-taxa approach can increase the effectiveness of taxon surrogacy and, therefore, the accuracy of recommendations when applying results to a wider group of taxa (Larrieu et al., 2018; Soliveres et al., 2016). Since sampling multiple taxa at the landscape scale requires more time, resources and expertise, studies of this scale rarely sample more than

one taxonomic group. Therefore, this study, which sampled four taxa, contributes greatly to our knowledge of biodiversity in forests. Overall vascular plant communities were relatively unresponsive to changes resulting from stand development, whereas spider and moss communities were more sensitive (Chapters 2 and 4). Notably, however, moss diversity in Sitka spruce forests had the opposite relationship with stand age to other taxonomic groups (Chapter 2). In addition, moss communities showed the strongest evidence for declines in diversity over the 20-year study period compared to carabids and vascular plants since declines were detected in all forest types (Chapter 3). Mosses are not able to control their water potential and so are more vulnerable to climate change as well as changes in microclimate due to structural changes within forests (Raabe et al., 2010). In addition, mosses are poor competitors relative to vascular plants and so are negatively impacted by increasing vascular plant cover where eutrophication occurs (Virtanen et al., 2017). Interestingly, the dominant spider family sampled in this study is also water-limited and this may explain why both of these taxa are particularly sensitive to changes in stand development (Kumschick et al., 2009). The conclusions drawn from this study would have differed if only one taxonomic group was studied, particularly if it was the most commonly studied vascular plant group. This highlights the value of including multiple taxa in research that seeks to assess impacts on biodiversity. This suggests caution should be used when including a single, so-called 'surrogate taxa', without firm evidence that the response of this taxa will be similar to other groups, since there is a high risk of drawing erroneous conclusions. For example, it has been suggested that carabids can be good surrogates for spiders since they are both generalist predators and carabids are easier to process (Cole et al., 2005). However, this study found spider diversity to be more sensitive than carabid diversity to structural changes during stand development in Scots pine and spider diversity responded more slowly to changes in Sitka spruce (Chapter 2). A carefully curated combination of multiple taxa may improve our understanding of ecosystems and their response to environmental change whilst still being cost-effective and logistically feasible.

The role of different forest types in supporting biodiversity

Forest studies can produce highly variable results, and this has been attributed to the structurally complex nature of this habitat which is influenced by stand stage, tree species and history (Hester et al., 2019). Therefore, multiple forest types, as well as multiple taxa, are needed for studies to produce an accurate estimate of forest biodiversity. Landscape scale forest studies such as this one, including multiple tree species at different stand stages are rare. This study also included Scots pine, a tree species that has received relatively little attention at this scale (but see Humphrey et al., 2003). Although trends varied among the taxonomic groups, communities in Sitka spruce and Oak forests were more negatively affected over time and, in Sitka spruce, through the forest harvest cycle than in Scots pine (Chapters 2, 3 and 4). This is thought to be the result of differences in the structural changes that take place during stand development and differences in light transmittance in the canopy of each tree species (Hale et al., 2009). Specifically, canopy closure is faster and more complete during Sitka spruce stand development, leading to the near-complete loss of forest floor vascular plants (Chapter 2). This affects primary consumers which are dependent on vascular plant cover and diversity, as well as their predators, and will also have implications for competition, microclimate and availability of shelter. These differences in structure were found to lead to different communities among forest types. For example, pre-thicket stands supported species typically associated with open habitats, while closed canopy stands supported more forest-specialists (Chapter 4). In addition, some traits were associated with different stages of the forest harvest cycle (e.g. large spiders and turf-forming mosses in young stands, sheet-web weaving spiders in closed canopy stands) (Chapter 2). Further, long term retention stands showed a varying ability to support more diverse communities than closed canopy stands of the same tree species (Chapters 2 and 4). Therefore, the variety of forest types in the landscape resulting from clearfell silviculture may increase diversity at the landscape-scale. However, clearfelling represents a major disturbance to forest ecosystems and is not considered to result in natural forest structure

(Carnus et al., 2006). Indeed, the less intensively managed oak forests in this study did support unique and rare spider species which are thought to be threatened by plantation establishment. In addition, mid-rotation and mature Sitka spruce stands supported little in the way of diverse or unique communities (Chapters 2 and 4). However, since changes in communities are thought to be related to stand structural changes which are not necessarily tied to canopy tree species, management action (e.g. thinning) could improve the ability of some forest types to support biodiversity. Along with stand structure, location was also often more important than forest type *per se* with differing species pools in the north and south of Great Britain driving much of the difference between communities (Chapters 2 and 4). Whilst this result is unsurprising, regional variation should be taken into account in future large-scale studies so that forest managers in different regions can better target management options for the available species pool.

Do common forest types support species of conservation concern?

Seven carabid species and 31 spider species of conservation concern were sampled during this study (Chapters 2, 3, and 4). All major forest types studied supported at least one species of conservation concern, with the exception of mature Sitka spruce which supported no rare spider species and long-term retention Sitka spruce which supported no rare carabid species. Rare species included those thought to be declining or threatened with declines in Great Britain and, although they were generally rare within the datasets, this study indicates that common forest types in Great Britain, including intensively managed plantations, have a role to play in their conservation. However, further research would enable us to distinguish whether these species are thriving, surviving or declining in these forests.

Evidence for UK Forestry Standard guidelines

This research contributes to the evidence base for the UK Forestry Standard. Evidence for the biodiversity requirements and guidelines addressed by this study are summarised in Table 5.1. We found mixed support for all applicable guidelines as a result of the differences

between responses of each taxonomic group but also because of differing influence among forest types (Chapters 2, 3 and 4). It is noteworthy that we found supporting evidence for clearfelling practice (Chapters 2 and 4). Alternatives are often recommended because clearfell and replanting is not thought to support biodiversity as well as other silvicultural practices such as shelterwood, group selection or other continuous cover forestry options since these are thought to produce forest structure and dynamics more like those of natural forests (Carnus et al., 2006). However, if clearfell practices were abandoned, this would remove young, open forest stands from the landscape. Whereas, these stands have been found to be of high value to biodiversity for a range of taxonomic groups and for open-habitat specialists. On the other hand, if the goal is to support forest specialists rather than high diversity, clearfell practices resulting in pre-thicket stands are not beneficial. The varying responses of taxa to forest management and varying goals of biodiversity conservation mean that there is unlikely to be one solution to suit all and so management that results in a range of stand structures and silvicultural approaches across the landscape is likely be best for biodiversity. Finally, we found that, for the taxonomic groups studied, tree species was not as important as stand structure. However, native forests, including semi-natural oak, supported unique species compared to plantation forests and so we should continue to prioritise the conservation of such habitats.

Table 5.1: Evidence for United Kingdom Forestry Standard (UKFS) guidelines and requirements based on results from this study. SP stands for Scots pine, SS for Sitka spruce, PT for pre-thicket, MR for Mid-rotation and M for mature stands. Data chapters in which evidence was found are indicated in parentheses.

UKFS guidance	**Evidence in support**			
	Vascular plants	**Mosses**	**Carabids**	**Spiders**
Long-term retention	NO Diversity lower or same as other stages in SS and SP (CH2)	MIXED Highest diversity in SS but lowest in SP (CH2)	MIXED Higher diversity than M/MR in SS only (CH2)	MIXED Higher diversity than M/MR in SP and increasing in SS (CH2)
Range of stand structures/ silvicultural approaches e.g. Pre-thicket resulting from clearfell	NO Similar traits/ diversity in all forest types (CH2) MIXED Higher diversity prior to canopy closure in SS (CH2)	YES Different traits/ diversity in different forest types (CH2) MIXED Lower diversity PT in SS but higher in SP (CH2)	MIXED Similar traits in different forest types but diversity varies (CH2) MIXED High diversity prior to canopy closure in SS (CH2)	YES Different traits/ unique communities/ species of conservation concern and diversity varies in different forest types (CH2, CH4) YES PT supports high diversity, unique functional traits and unique species & species of conservation concern in SS and SP (CH2 CH4)
Native trees are better for biodiversity	MIXED Similar response to harvest cycle in SP and SS but SP more diverse (CH2)	MIXED Respond differently in SS and SP but diversity similar (CH2)	MIXED Diversity negatively affected by harvest cycle in SS but similar diversity (CH2)	NO Similar response to harvest cycle in SP and SS and similar diversity (CH2) Stand structure more important than tree species (CH4)
Maintain semi-natural/ ancient forest	YES Support unique species (CH3)	MIXED Support few unique species (CH3)	MIXED Support some unique species (CH3)	YES Support unique species of conservation concern (CH4)

Further study

Recent evidence suggests that interspecific trait variation does not always vary more than intraspecific variation, therefore future studies should explore the possibility of measuring individual-based rather than species-based functional traits (Albert et al., 2011). Individual-based trait measurement may provide more insights than species-based since some traits show a response at this level rather than at species level (e.g. plant height, wing-form, body size, moss life-form). Additionally, since selection works at the individual rather than species level, this is where we are likely to detect changes first. This method does not limit trait selection to the set of known and measured traits for any organism, which is of benefit when sampling lesser studied taxa. However, whilst this level of information can be highly informative, the collection of individual-based trait data is much more time-consuming than using existing trait databases and will likely require compromise in other areas of the study design (e.g. replication, regional scale or number of taxonomic groups included). In addition, functional effect traits should be explored since this will give insight into the effects on ecosystem services and functions which are of great interest to humanity (Violle et al., 2007). This is only likely to be possible for well-studied taxonomic groups such as vascular plants, since we do not fully understand the effect of other taxonomic groups on ecosystem services or know how to measure this. We plan to explore this concept using the data collected here on vascular plant communities using their effect traits in combination with response traits to determine the resilience of ecosystem services.

In this study there was mixed evidence of biotic homogenisation, despite finding evidence of some of the processes involved in biotic homogenisation (e.g. increased dominance of widespread, generalist species). Further clarity may be gained by a longer study period since biotic homogenisation has been detected in forests over longer time periods (at least 45 years between sampling periods). Therefore, it would be of value to continue to monitor these study plots into the future. In addition, this would allow us to determine whether forest

stands managed in long-term retention provide value in addition to other stand types in terms of their biodiversity value.

The multi-taxa approach taken here proved to be more valuable than if any of the taxa included were studied alone. However, our understanding would be improved further by studying additional trophic levels (e.g. detritivores and herbivores). In particular, herbivorous and saproxylic taxa are likely to have closer relationships with tree species than any of the taxa studied here since they have often evolved to utilise single species or genera of plants. Similarly, this study only sampled epigeal spiders whereas spiders are known to inhabit all layers of the forest (Oxbrough et al., 2005). Spiders living in the canopy may also be more strongly influenced by canopy tree species than epigeal spiders. Indeed, higher abundance and SR of spiders have been found in tree canopies with more complex branch structure (Halaj et al., 1998).

As indicated by this study, it may be possible to improve the ability of some forest stands to support biodiversity by altering their management. In order to make more prescriptive recommendations, further exploration of the effect of different management options on biodiversity is required. Opening of the canopy in Sitka spruce stands may achieve higher diversity during stand development. This could be achieved by, for example, thinning at different stages of development or wider spaced planting to produce lower stand densities. However, this may have adverse effects on other aspects of biodiversity and habitat provisioning in these stands including deadwood volumes and quality, and increased disturbance frequency. If the prevention of near complete canopy closure is valuable for biodiversity in Sitka spruce stands, it will also be important to determine the desirable level of canopy cover to aim for. Since canopy closure was rapid in these stands and no thinning took place, it was not possible to sample thoroughly at the low canopy cover end of the gradient. Therefore, it would be valuable to study communities of multiple taxonomic groups in Sitka spruce stands with a wide range of levels of canopy cover.

Concluding remarks

This study found that common forest types in Great Britain, including non-native plantation, native plantation and native forest all have a role in supporting biodiversity, although this was not always the case in the most closed-canopy Sitka spruce stands, where environmental filtering had a stronger effect on biodiversity. Further, canopy tree species was not as important as location or stand structure in determining diversity or community composition, suggesting that alternative management could be implemented where there is a desire to improve a forest's ability to support biodiversity. Finally, long-term changes in diversity in common forest types in Great Britain suggest that the processes leading to biotic homogenisation are occurring, especially in oak forests, where there was evidence of declining diversity in multiple taxonomic groups. Therefore, even in habitats managed for conservation purposes, species declines are occurring over time with the potential for biotic homogenisation in the future.

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